

## The *Anacroneuria* of Costa Rica and Panama (Insecta: Plecoptera: Perlidae)

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**Abstract.**—Twenty seven *Anacroneuria* species are recorded for Costa Rica and Panama including 18 described as new species (*Anacroneuria alajuela*, *A. benedettoi*, *A. curiosa*, *A. exquisita*, *A. hacha*, *A. harperi*, *A. holzenthalii*, *A. marca*, *A. marginata*, *A. maritza*, *A. perplexa*, *A. talamanca*, *A. tornada*, *A. uatsi*, *A. varilla*, *A. ventana*, *A. zapata*, *A. zarpa*). Redescriptions are given for nine species previously recorded from the area. Lectotypes are designated for *Anacroneuria expansa* Klapálek, *A. annulipalpis* Klapálek, *A. planicollis* Klapálek and *A. plutonis* (Banks); *A. expansa* Klapálek = *A. acutipennis* Klapálek, *A. chiapasa* Jewett = *A. planicollis* Klapálek, *A. dampfi* Jewett = *A. planicollis* Klapálek, and *A. tristani* (Navas) = *A. plutonis* (Banks) are placed in synonymy. A provisional key for males is provided.

The stonefly fauna of lower Mesoamerica includes only the speciose neotropical perlid genus *Anacroneuria*. Despite sporadic attempts (e.g., Needham & Broughton 1927, Jewett 1958, Harper 1992) this fauna remains virtually undocumented. Eleven of the twelve previously proposed Costa Rican and Panamanian species are known from obscure, scattered and undiagnostic original descriptions published early in this century. At that time the importance of internal male genitalic characters was unrecognized and similarities in size, coloration and subgenital plate structure led to the erroneous concept of *Anacroneuria* species with ranges extending from Mexico to Brazil (Needham & Broughton 1927). More recent studies (Zwick 1972, 1973; Stark 1995) suggest the male aedeagal structure is the most reliable structure for species recognition in this genus. Egg shape and size are useful in distinguishing some species but the chorionic surface lacks the detail found in other perlids.

In addition to the 12 species whose holotypes or lectotypes are based on Costa Rican or Panamanian material, Needham & Broughton (1927), Jewett (1958) and Harp-

er (1992) include records of three earlier described species and records of three species based on paratypes. Needham & Broughton (1927) and Jewett (1958), for example, both record *A. cincta* (Pictet) and *A. nigrocincta* (Pictet) from the region but Zwick (1972, 1973) has shown neither of these can be considered valid records. Because the holotype of *A. cincta* is lost, that species is considered a nomen dubium, and the species identified as *A. nigrocincta* in these studies applies to another, presently unidentified species. Harper's (1992) record of *A. cincta* from Panama is based on Needham & Broughton's (1927) invalid definition of the species. Jewett (1958) included Panamanian specimens among the paratypes of *A. crenulata* Jewett and *A. flavomarginata* Jewett. Harper's (1992) figures of the male aedeagi of these specimens indicate they are distinct from the respective allotypes. These specimens are assigned to two of the new species described in this study. Unfortunately the specimen listed by Harper (1992) as the putative male of *A. pallida* Jewett could not be located. *Anacroneuria sulana* Needham & Broughton (1927), recorded by Jewett (1958) from Panama, was

placed as a synonym of *A. annulicauda* (Pictet) by Zwick (1972). Jewett's Panamanian specimens, presumably in the American Museum of Natural History, need to be reexamined before this identification is accepted.

During the late 1980's and early 1990's, R. W. Holzenthal and colleagues at the University of Minnesota and D. H. Funk, J. Jackson and colleagues at the Stroud Water Research Center made extensive light trap collections of Costa Rican stoneflies. This valuable material was made available for my study and has been supplemented with specimens from the museums listed below. Results from available material indicate a minimum of 27 species occur in Costa Rica and Panama. This includes nine of the earlier named species and 18 that are new to science. A relatively strong pattern of endemism emerges from this study with 21 species known only from Costa Rica-Panama. None of the species reported in Costa Rica or Panama are known to occur in South America and only two are currently reported from Mexico (Jewett 1958, Stark 1995). Males of thirteen species were taken in light traps from a single locality at Estacion Maritza in Guanacaste Province.

#### Materials and Methods

Aedeagai and female terminalia were prepared by clipping the abdomen and placing it in a small beaker of KOH. The solution was brought to a boil, then the terminalia were placed in dishes of distilled water and extraneous tissue removed with fine forceps. The aedeagus was also removed from the abdominal cavity with fine forceps and figures were prepared in dorsal, ventral and lateral aspects at 100 $\times$ ; figures of the male ninth sternum were drawn at 50 $\times$  and the female terminalia at 25 $\times$ . Figures of the adult head and pronota were drawn at 25 $\times$  from specimens in alcohol.

Aedeagal preparations for scanning electron microscopy were made by crudely dissecting the structure from specimens in al-

cohol. The aedeagi were sonicated in acetone for one minute, air dried, placed on specimen stubs with double stick copper tape, sputter coated with gold-palladium, and the apex examined in ventral and lateral aspect with an AMRAY 1810D scanning electron microscope.

Holotype specimens of new species are placed in the United States National Museum (USNM); some specimens designated as holotypes are placed in the United States National Museum through the courtesy of Brigham Young University, Stroud Water Research Center, University of Minnesota and Utah State University. Paratypes and other specimens are deposited in the following collections as indicated:

Bill P. Stark, Clinton, Mississippi (BPS); Brigham Young University, Provo, Utah (BYU); C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado (CSU); Cornell University, Ithaca, New York (CU); Florida State Collection of Arthropods, Gainesville, Florida (FSCA); Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica (INBIO); Museum National d'Histoire Naturelle, Paris (MNHN); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of Natural History, Prague (NMP); Ohio State University, Columbus, Ohio (OSU); Stroud Water Research Center, Avondale, Pennsylvania (SWRC); University of Minnesota, Saint Paul, Minnesota (UMSP); Utah State University, Logan, Utah (USU).

#### Provisional Key to Regional Male *Anacroneuria*

1. Median pronotal band brown (Fig. 36) ..... 2
- Median pronotal band yellow, or pronotum without distinct pigment bands ..... 7
2. Hammer a low indistinct mound (Fig. 47) ..... *hacha*
- Hammer well developed, thimble or nipple shaped (Figs. 7, 62) ..... 3
3. Aedeagal apex projecting ventrally be-

tween hooks (Fig. 108); dorsal aedeagal keel absent ..... *tornada*

— Aedeagal apex not projecting between hooks (Fig. 93); dorsal aedeagal keel well developed (Fig. 94) ..... 4

4. Aedeagal apex with three subequal lobes (Fig. 95) ..... *planicollis*

— Aedeagal apex simple or with minute lateral lobes (Figs. 65, 85) ..... 5

5. Aedeagal apex beyond shoulders at least twice as long as wide (Fig. 84) ..... *maritza*

— Aedeagal apex beyond shoulders about as long as wide (Fig. 64) ..... 6

6. Lateral aspect of aedeagal apex wider than long at widest point (Fig. 38) ..... *divisa*

— Lateral aspect of aedeagal apex longer than wide (Fig. 63) ..... *lineata*

7. Hammer poorly developed or absent (Fig. 47) ..... 8

— Hammer thimble shaped, well developed (Fig. 7) ..... 12

8. Forewing length 7–11 mm ..... 9

— Forewing length at least 14 mm ..... 10

9. Aedeagal apex trilobed, lateral lobes small, hooks chelate (Fig. 90) ..... *perplexa*

— Aedeagal apex simple, hooks slender (Fig. 130) ..... *varilla* in part

10. Hammer absent (Fig. 67); aedeagal apex simple, usually with a sharp transverse keel (Fig. 68) ..... *magnirufa*

— Hammer a low obscure mound (Fig. 2); aedeagal apex trilobed, without keel (Fig. 4) ..... 11

11. Mesal lobe of aedeagal apex deeply notched (Fig. 4); wing membrane without transparent circular spot near cord ..... *acutipennis*

— Mesal lobe of aedeagal apex rounded (Fig. 44); wing membrane with transparent circular spot near cord ..... *exquisita*

12. Head without brown pigment spot between or just anterior to ocelli (Fig. 11) ..... 13

— Head with brown pigment between or just anterior to ocelli (Figs. 76, 96) ..... 16

13. Aedeagal apex and hooks asymmetrical (Figs. 53–55) ..... *harperi*

— Aedeagal apex and hooks symmetrical ..... 14

14. Median yellow pronotal stripe less than a fourth of pronotal width (Fig. 131); aedeagal apex with clawlike dorsolateral lobes (Fig. 134) ..... *zarpa*

— Median yellow pronotal stripe about half of pronotal width (Figs. 11, 31); aedeagal apex without clawlike dorsolateral lobes ..... 15

15. Dorsal aedeagal apex acute and simple (Fig. 14) ..... *annulipalpis*

— Dorsal aedeagal apex rounded and trilobed (Fig. 34) ..... *curiosa*

16. Aedeagal apex massive with winglike shoulders (Figs. 20, 60) ..... 17

— Aedeagal apex small and without winglike shoulders (Fig. 114) ..... 18

17. Lateral aedeagal wings large and pointed (Fig. 60) ..... *holzenthali*

— Lateral aedeagal wings small and rounded (Fig. 20) ..... *benedettoi*

18. Forewing length at least 13 mm ..... 19

— Forewing length no more than 10 mm ..... 22

19. Aedeagal apex with small dorsolateral lobes, apex shoe shaped in lateral aspect (Figs. 128–129) ..... *zapata*

— Aedeagal apex without dorsolateral lobes, lateral aspect not shoe shaped ..... 20

20. Dorsal aedeagal keel well developed (Fig. 124); wing membrane usually with a circular transparent spot at cord ..... *ventana*

— Dorsal aedeagal keel absent (Fig. 74); wing membrane without circular transparent spot ..... 21

21. Aedeagal apex gradually narrowed to tip, bases of aedeagal hooks bulging (Fig. 100); M-line and lateral callosities on head distinct (Fig. 96) ..... *plutonis*

— Aedeagal apex with almost parallel sides distal to shoulders, bases of hooks not enlarged (Fig. 75); head pattern with M-line and callosities indistinct (Fig. 71) ..... *marca*

22. Ventral aedeagal apex with prominent pair of membranous lobes (Fig. 120) ..... 23

— Ventral aedeagal apex without membranous lobes (Fig. 10) ..... 24

23. Aedeagal apex offset from shoulders by lateral notches, tip acute (Fig. 24) ..... *blanda*

— Aedeagal apex without lateral notches,

tip truncate or emarginate (Fig. 119) ..... *varilla* in part

24. Aedeagal apex projecting fingerlike from shoulders (Figs. 114–115) ..... *uatsi*

— Aedeagal apex not fingerlike, lateral margins more or less convergent to tip (Figs. 10, 80) ..... 25

25. Aedeagal apex with a U-shaped dorsal keel (Fig. 9) ..... *alajuela*

— Aedeagal apex without U-shaped keel ..... 26

26. Aedeagal apex gradually narrowed from bases of hooks to near tip (Fig. 104) ..... *talamanca*

— Aedeagal apex not conspicuously narrowed beyond hooks (Figs. 29, 80) .. 27

27. Aedeagal apex with well developed dorsal keel (Fig. 79); area beyond hooks about as wide as long (Fig. 80) ..... *marginata*

— Aedeagal apex with obscure dorsal keel (Fig. 29); area beyond hooks longer than wide (Fig. 30) ..... *costana*

*Anacroneuria acutipennis* Klapálek  
Figs. 1–5, 136, 159–160

*Anacroneuria acutipennis* Klapálek, 1923:  
23. Holotype ♀, Volcan Chiriquí, Panama (NMP).

*Anacroneuria expansa* Klapálek, 1923:22.  
Lectotype ♀, Guatemala (NMP), new synonymy.

*Anacroneuria* sp. C: Harper, 1992:118.

*Adult habitus*.—Head yellow except for lappets and dark area forward of ocelli. Pale median pronotal stripe wide, midlateral dark stripes irregular (Fig. 1). Wing membrane transparent, veins pale brown; C and Sc pale.

*Male*.—Forewing length 16–17 mm. Hammer a low mound (Fig. 2). Aedeagal apex trilobed, mesal lobe deeply notched. Hooks stout, dorsal keel absent (Figs. 3–5, 159–160).

*Female*.—Forewing length 19–21 mm. Subgenital plate bilobed, lobes broad and usually emarginate; notch V-shaped. Transverse sclerite of sternum nine well developed; mesal sclerite T-shaped, lateral setae prominent (Fig. 136).

*Nymph*.—Unknown.

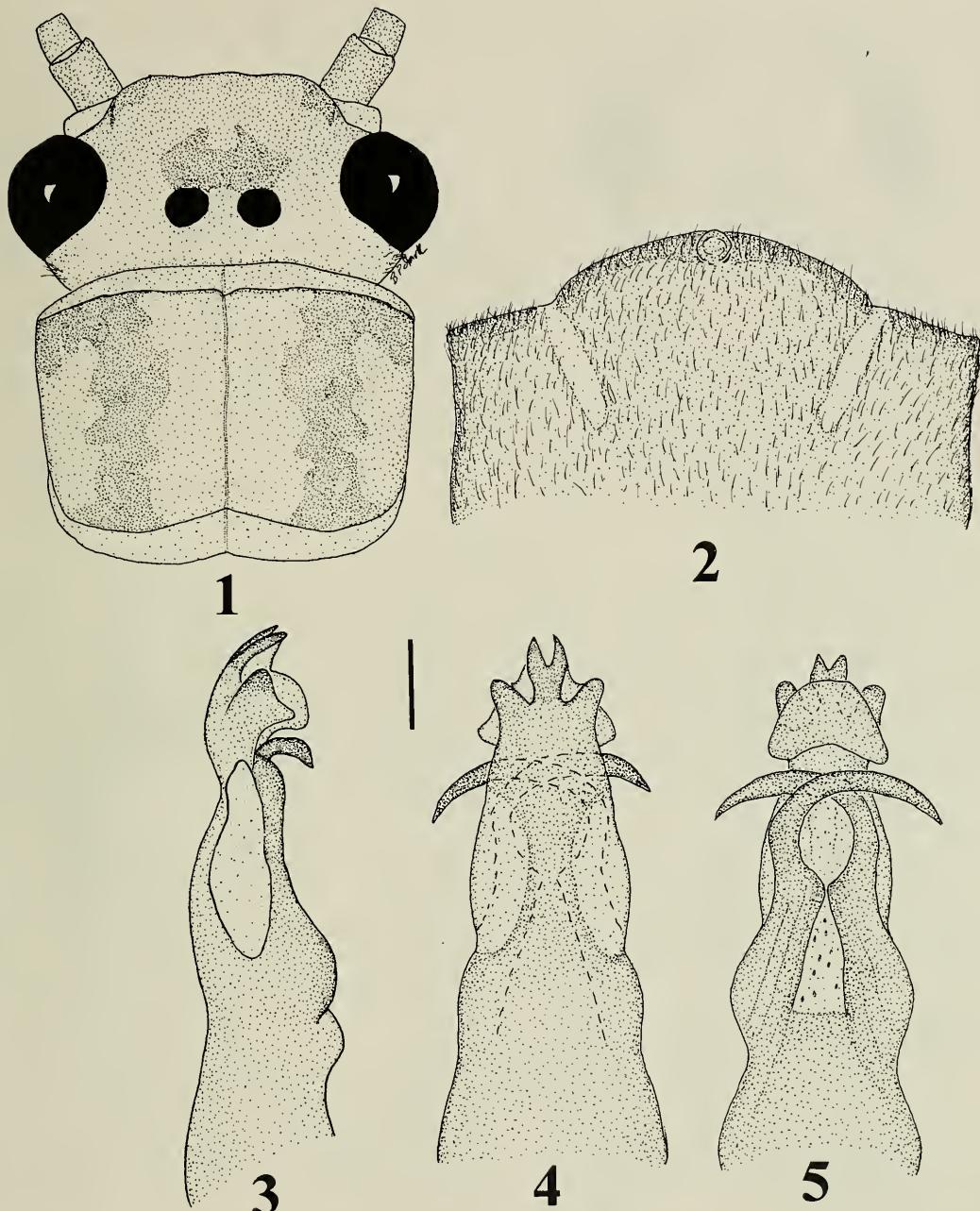
*Material*.—Costa Rica: Alajuela: Rio Peje, 1 km SE San Vicente, 1450 m, 14 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 1 ♂, 1 ♀ (UMSP). Cartago: Reserva Tapanti, Quebrada Palmitos, 1400 m, 2 Jun 1990, R. Holzenthal, R. Blahnik, F. Munoz, 1 ♂, 3 ♀ (BPS). Same location, 24 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 3 ♂ (INBIO). Same location, 1 Aug 1990, 3 ♀ (UMSP). Puntarenas: Rio Bellavista, ca. 1.5 mi NW Las Alturas, 1400 m, 8 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (USNM). San Jose: Parque Nacional Braulio Carrillo, Rio Zurqui, 1650 m, 6 Jul 1986, R. Holzenthal, M. Heyn, B. Armittage, 1 ♂ (BPS). Guatemala: No locality data, *A. expansa* lectotype ♀ (NMP). Panama: Volcan Chiriquí, 1907, V. D. Whede, holotype ♀ (NMP). Same locality, 5500', 11 Jan 1964, S. L. Wood, 2 ♂ (BYU).

*Comments*.—A female specimen bearing label data “*Anacroneuria expansa* Klap. 1923, guat/de Selys 21” from the Natural History Museum, Prague, is selected as lectotype. Although the forewing length of this specimen is given as 28 mm (Klapálek 1923) it is similar in body size to other specimens of *A. acutipennis*, and it is indistinguishable from these specimens in subgenital plate shape and features of sternum nine and thus is placed as a synonym. The Panamanian material recorded as “*Anacroneuria* sp. C” by Harper (1992) is also assigned to this species.

*Anacroneuria alajuela*, new species  
Figs. 6–10

*Adult habitus*.—Head with a large dark area over ocelli extending to M-line; lappets brown. Median pronotal stripe yellow, lateral stripes brown (Fig. 6). Wing membrane brown, veins brown.

*Male*.—Forewing length 9 mm. Hammer thimble shaped, height greater than basal diameter (Fig. 7). Aedeagal apex broad, scoop shaped and bearing a dorsal U-



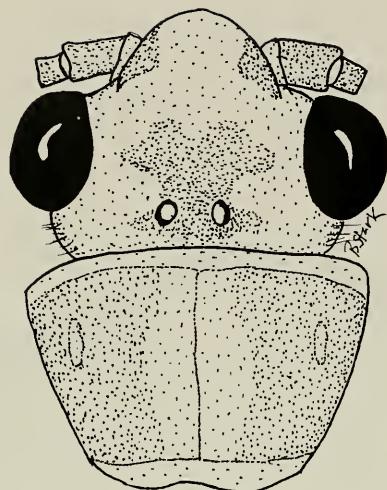
Figs. 1-5. *A. acutipennis* structures. 1. Head and pronotum. 2. Male sternum. 3. Aedeagus, lateral. 4. Aedeagus, dorsal. 5. Aedeagus, ventral. Scales: 0.6 mm (1), 0.3 mm (2), 0.15 mm (3-5).

shaped keel; hooks moderately thickened (Figs. 8-10).

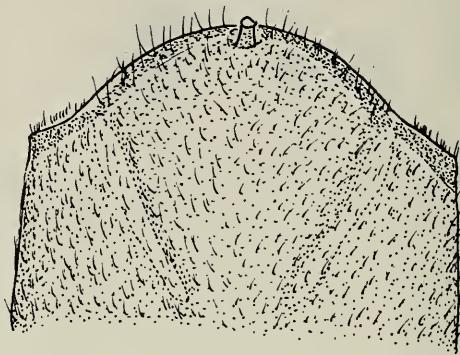
*Female*.—Unknown.

*Nymph*.—Unknown.

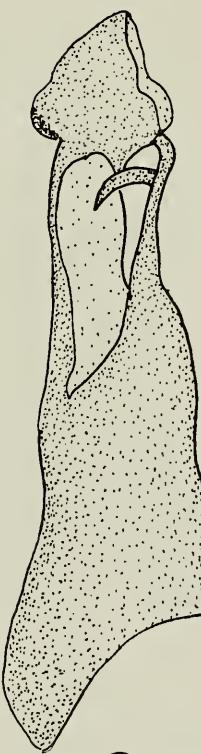
*Etymology*.—The species name, based on the Costa Rican province in which the holotype was collected, is used as a noun in apposition.



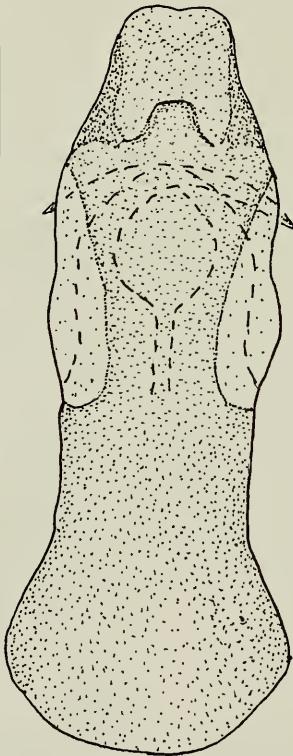
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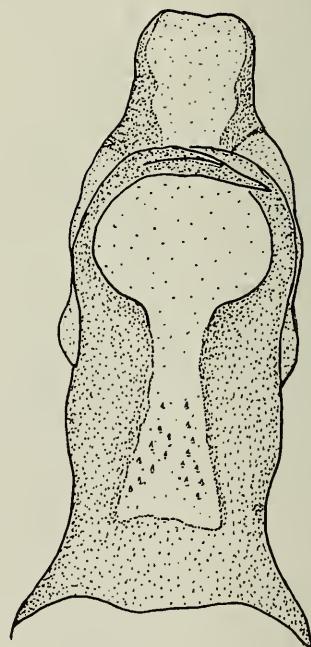
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Figs. 6-10. *A. alajuela* structures. 6. Head and pronotum. 7. Male sternum. 8. Aedeagus, lateral. 9. Aedeagus, dorsal. 10. Aedeagus, ventral. Scales: 0.6 mm (6), 0.3 mm (7), 0.15 mm (8-10).

**Types.**—Holotype ♂ from Costa Rica, Alajuela, 20 km S Upala, June 1990, F. D. Parker (USNM).

**Diagnosis.**—The broad aedeagal apex is similar to that of *A. divisa* (Figs. 38–40) and *A. lineata* (Figs. 63–65) but these species have dark mesal pronotal stripes, low moundlike hammers and narrow longitudinal aedeagal keels.

*Anacroneuria annulipalpis* Klapálek

Figs. 11–15, 137, 161–162

*Anacroneuria annulipalpis* Klapálek, 1922: 91. Lectotype ♀, Chiriquí, Panama (NMP).

*Anacroneuria quadriloba* Jewett: Harper, 1992:117.

**Adult habitus.**—Head yellow. Pronotum yellow except for irregular, dark lateral stripes (Fig. 11). Wing membrane pale amber, veins C, Sc pale, others brown.

**Male.**—Forewing length 12–16 mm. Hammer thimble shaped (Fig. 12). Aedeagal apex greatly narrowed into curved spine; ventral membranous processes present. Dorsal keel absent, hooks scooped at apex (Figs. 13–15, 161–162).

**Female.**—Forewing length 16–20 mm. Subgenital plate four lobed; outer lobes broad, but subequal in length to inner lobes. Transverse sclerite of sternum nine curved, mesal sclerite T-shaped and sparsely setose (Fig. 137).

**Nymph.**—Unknown.

**Material.**—Costa Rica: Alajuela: Reserva Forestal San Ramon, Rio San Lorencito, 980 m, 30 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (UMSP). Same location, 1 May 1990, R. Holzenthal, R. Blahnik, 1 ♀ (UMSP). Guanacaste: Estacion Maritza, Rio Tempisque, 5 May 1989, 7 ♂ (BPS). Same location, 11 May 1990, 1 ♂, 1 ♀ (SWRC). Same location, 30 May 1990, 2 ♂ (SWRC). Same location, 22 Oct 1990, 5 ♂ (INBIO). Puntarenas: Zona Protectora Las Tablas, Rio Coton, Sitio Coton, 1460 m, 15 Apr 1989, R. Holzenthal, R. Blahnik, 1 ♂, 1 ♀ (INBIO). Rio Bella-

vista, ca. 1.5 km NW Las Alturas, 1400 m, 2 Aug 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂, 3 ♀ (UMSP). Rio Jaba, 1.4 km W Las Cruces, 1150 m, 14 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂ (BPS). San Vito de Java, 23 May 1960, C. F. Dowling, 1 ♂ (FSCA). San Jose: Parque Nacional Braulio Carrillo, Rio Zurqui, 1650 m, 6 Jul 1986, R. Holzenthal, M. Heyn, B. Armitage, 2 ♂, 1 ♀ (UMSP). El Salvaje, Rio Tabarcia, 8 km E Palmichal, 1650 m, 19 Jan 1992, R. Holzenthal, K. Kjer, F. Quesada, 2 ♂ (INBIO). Panama: Chiriquí Province, 5 km NE El Hato del Volcan, 1 Oct 1975, D. Chandler, 1 ♂ (BYU). Volcan Chiriquí, 5500' 11 Jan 1964, S. L. Wood, 2 ♂ (BYU). Chiriquí, 2 ♀ syntypes (NMP).

**Comments.**—Two female syntypes were located, each with damaged subgenital plates. One specimen is so severely damaged as to prevent diagnosis. The other has the left half of sternum eight and most of sternum nine intact and is chosen as lectotype. Both specimens are in the National Museum of Natural History, Prague and were studied while on loan to P. Zwick. Female *A. quadriloba* Jewett are indistinguishable from this species but the aedeagus of paratotypes are more similar to those of *A. lineata* (Fig. 95). However, the Panamanian records listed for *A. quadriloba* by Harper (1992) are to be included with this species.

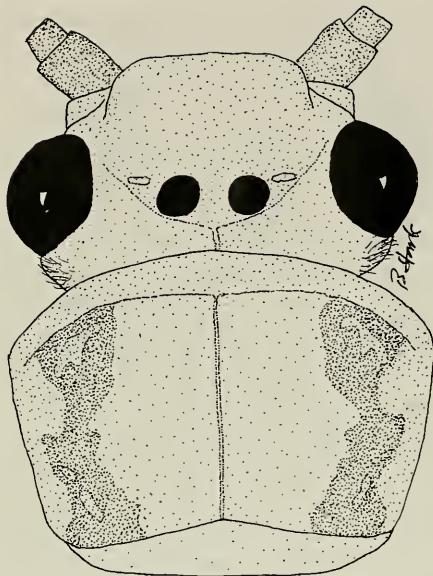
Costa Rican specimens show somewhat more size variation than has been noted for other *Anacroneuria*.

*Anacroneuria benedettoi*, new species

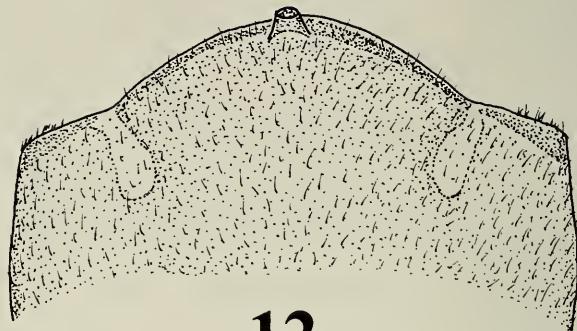
Figs. 16–20, 138, 163–164

**Adult habitus.**—Head mostly yellow brown with diffuse brown over ocelli and lappets. Median yellow pronotal stripe bordered by irregular, broad midlateral brown bands; anterolateral margins pale (Fig. 16). Wing membrane brown, veins brown.

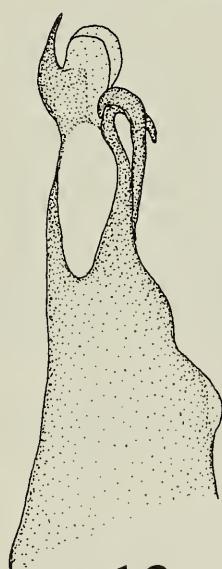
**Male.**—Forewing length 10 mm. Hammer thimble shaped, height subequal to diameter (Fig. 17). Aedeagal apex trilobed,



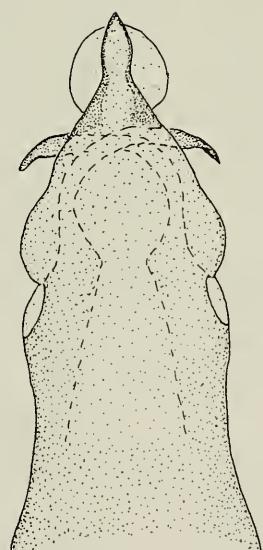
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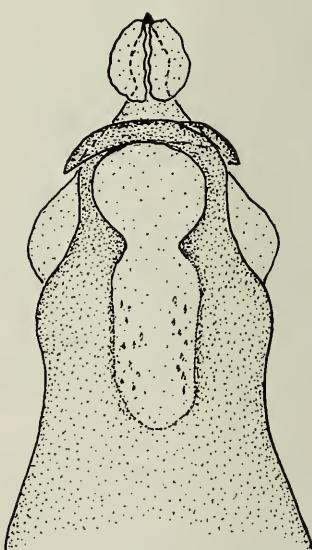
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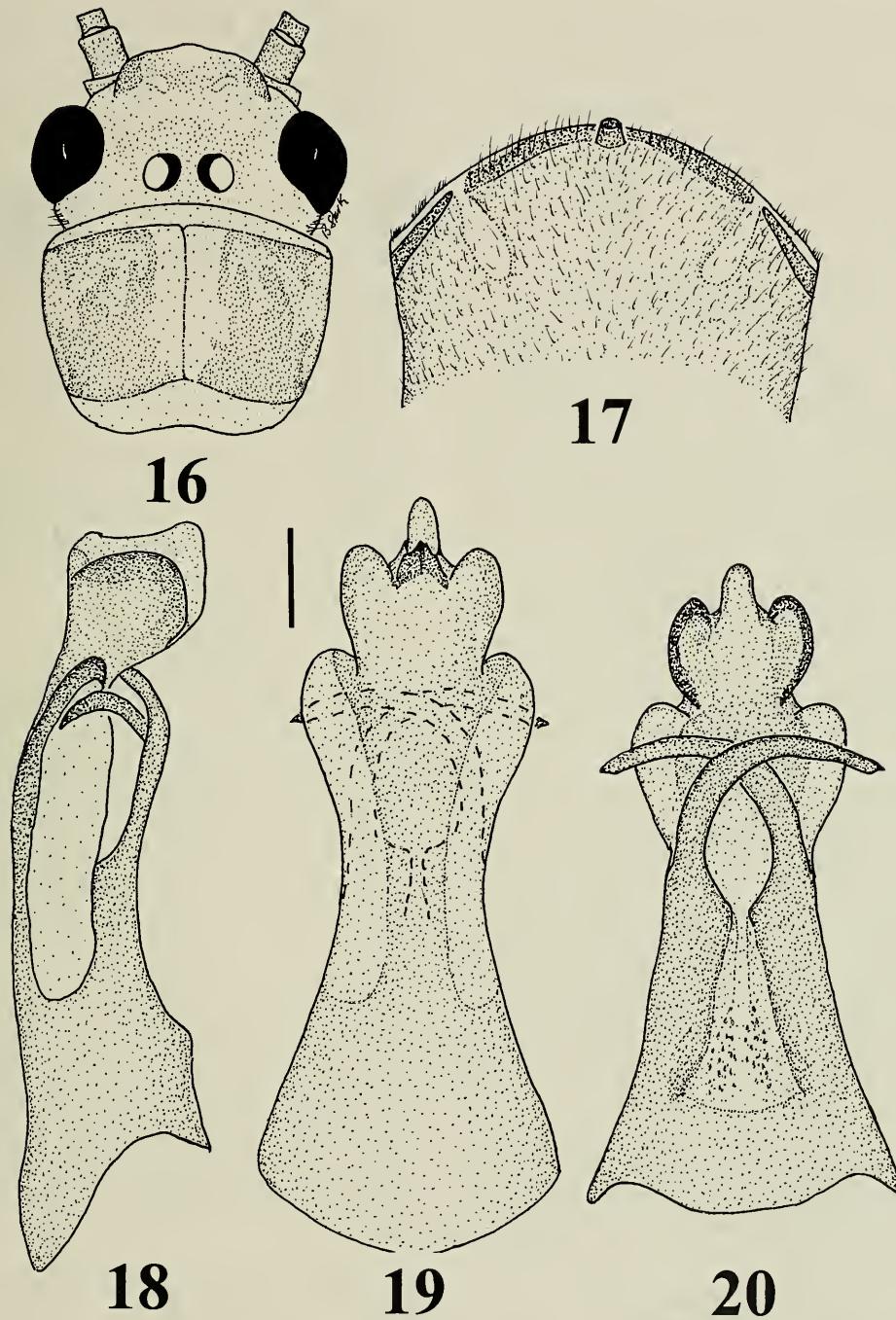
Figs. 11-15. *A. annulipalpis* structures. 11. Head and pronotum. 12. Male sternum 9. 13. Aedeagus, lateral. 14. Aedeagus, dorsal. 15. Aedeagus, ventral. Scales: 0.6 mm (11), 0.3 mm (12), 0.15 mm (13-15).

shoulders projecting laterally. Dorsal keel on mesal lobe, hooks slender (Figs. 18-20, 163-164).

*Female*.—Forewing length 12-13 mm. Subgenital plate four lobed. Lateral lobes

longer than mesal lobes, mesal notch V-shaped. Transverse sclerite of sternum nine sinuate; T-shaped mesal sclerite setose, lateral setae prominent (Fig. 138).

*Nymph*.—Unknown.



Figs. 16-20. *A. benedettoi* structures. 16. Head and pronotum. 17. Male sternum. 18. Aedeagus, lateral. 19. Aedeagus, dorsal. 20. Aedeagus, ventral. Scales: 0.6 mm (16), 0.3 mm (17), 0.15 mm (18-20).

**Etymology.**—The patronym honors L. A. Benedetto for his generosity in sharing information on *Anacroneuria* type material.

**Types.**—Holotype ♂ from Costa Rica, Guanacaste, Rio Los Ahogados, 11.3 km ENE Quebrada Grande, 470 m, 7 Mar 1986, R. Holzenthal, W. Fasth (USNM). Paratypes: Costa Rica: Alajuela: Laguna Rio Cuarto, 2.8 km N Rio Cuarto, 400 m, 13 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 2 ♂ (UMSP). Guanacaste: Rio Gon- gora, 4 km NE Quebrada Grande, 590 m, 21 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 6 ♂ (INBIO, UMSP). Rio Aguacate, 0.5 km E Aguacate, 590 m, 16 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 1 ♂ (UMSP). Rio Orosi, Estacion Pitilla, 700 m, 22 May 1990, R. Holzenthal, R. Blah- nik, 2 ♂ (BPS). Parque Nacional Guana- caste, El Hacha, Quebrada Alcornoque, 250 m, 26 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 9 ♂ (BPS). Estacion Maritza, Rio Tempisquito, 28 May 1989, 1 ♂ (SWRC). Limon: Rio Banano, 16 km WSW Bomba, 150 m, 26 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 8 ♂ (UMSP). Puntarenas: Reserva Biologica Carara, Quebrada Bonita, 35 m, 18–20 May 1990, R. Holzen- thal, R. Blahnik, 1 ♂ (UMSP). 2 mi SW San Vito de Java, 22–24 Jun 1964, R. Woodruff, 2 ♂ (FSCA). San Jose: Reserva Biologica Carara, Rio Carara, Carara, 280 m, 14 Feb 1991, R. Holzenthal, F. Munoz, J. Huisman, 2 ♂, 1 ♀ (UMSP). Panama: Bocas del Toro Province: Miramar, 3 Apr 1979, H. Wolda, 1 ♂ (BYU).

**Diagnosis.**—This species is similar to *A. holzenthalii* but has smaller and apically rounded aedeagal wings rather than long and pointed wings typical of *A. holzenthalii*.

*Anacroneuria blanda* Needham & Broughton  
Figs. 21–25, 139

*Anacroneuria blanda* Needham & Broughton, 1927:117. Holotype ♀, Barro Col- rado Island, Panama (CU).  
*Anacroneuria blanda*: Harper, 1992:117.

**Adult habitus.**—Head yellow except for lappets and dark area covering ocelli and extending forward and laterally to M-line. Median pronotal stripe yellow, lateral stripes brown, anterolateral margins pale (Fig. 21).

**Male.**—Forewing length 9 mm. Hammer cylindrical, height greater than diameter (Fig. 22). Triangular aedeagal apex offset from shoulders by transverse dorsolateral grooves; ventral aspect with a pair of membranous lobes, lateral aspect sinuate. Dorsal keel absent, hooks somewhat scoop shaped at the tips (Figs. 23–25).

**Female.**—Forewing length 13–14 mm. Subgenital plate bilobed, margins rounded or truncate, notch V-shaped. Transverse sclerite of sternum nine absent, posterior margin concave; mesal sclerite triangular and sparsely setose (Fig. 139).

**Nymph.**—Unknown.

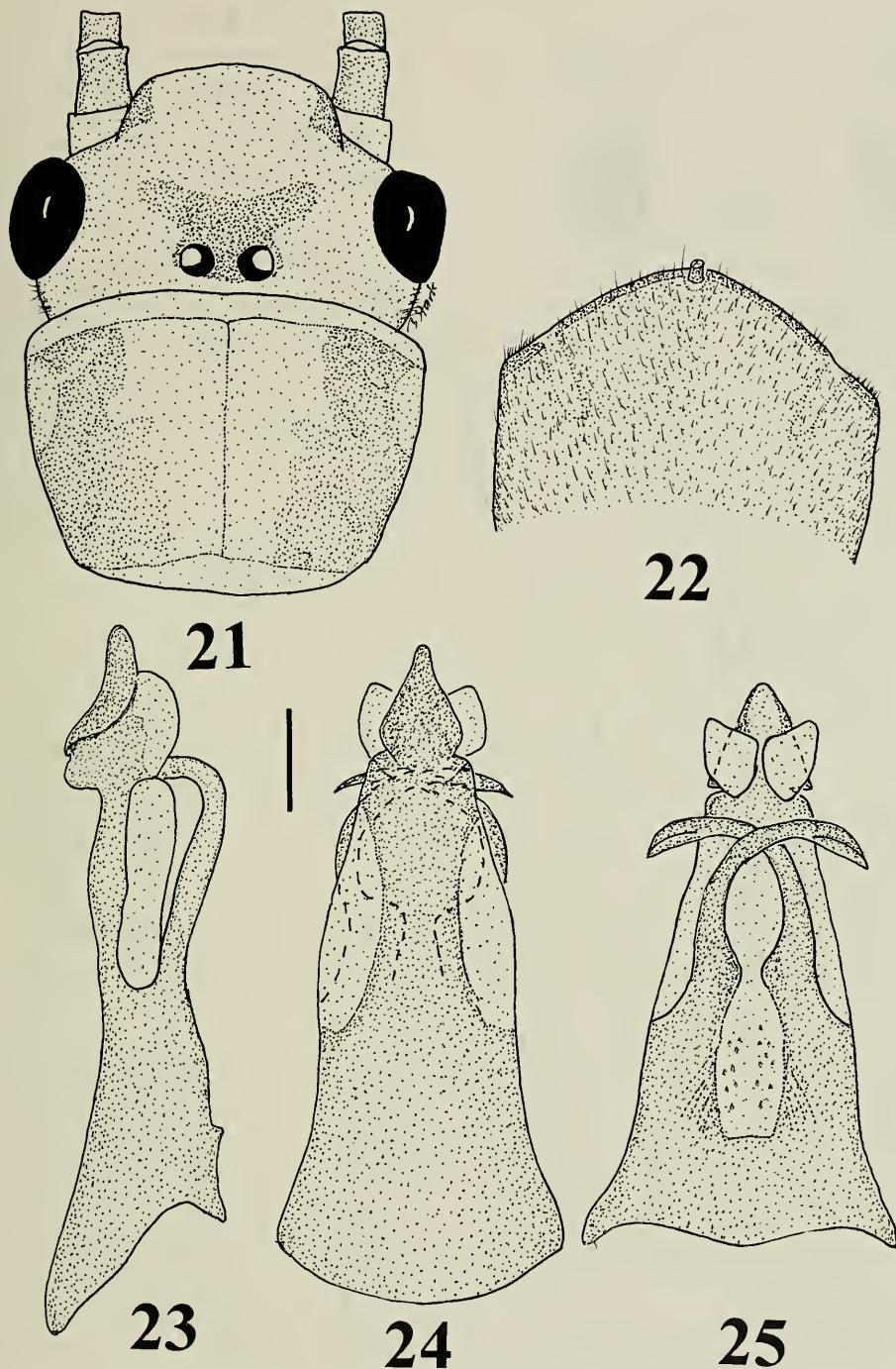
**Material.**—Costa Rica: Alajuela: 20 km S Upala, 5–10 Mar 1991, F. Parker, 2 ♂ (BYU, USU). Puntarenas: 2.8 mi E Golfito, 3–4 Jul 1967, O. S. Flint, Ortiz, 1 ♂ (USNM). Panama: Rio Agua Salud, Pipe- line Road, 8–12 Jul 1967, O. S. Flint, Ortiz, 1 ♂ (USNM). Cerro Campana, 11–14 Jul 1967, O. S. Flint, 2 ♀ (USNM). Barro Col- rado Island, W. C. Allee, Holotype ♀ (CU).

**Comments.**—*Anacroneuria blanda* was known from the holotype female until Harper (1992) assigned the additional Pan- amanian specimens listed above to this species. Although these specimens have a larger area of dark pigment on the head than the holotype, they are indistinguishable in other features and I concur with this place- ment.

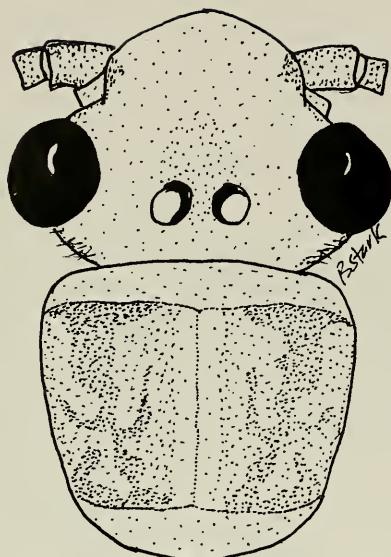
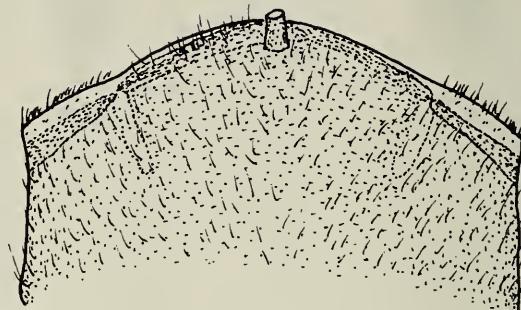
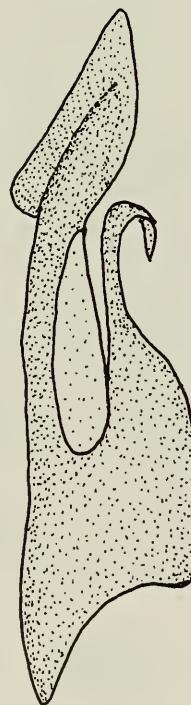
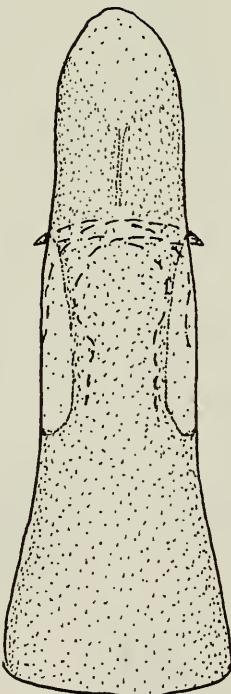
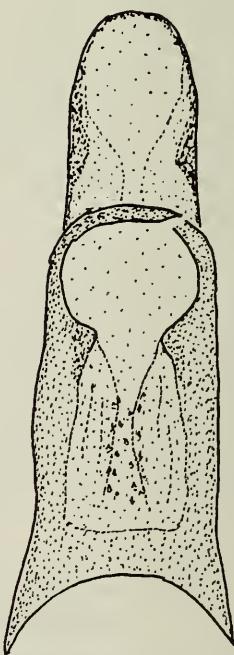
*Anacroneuria costana* (Navas)  
Figs. 26–30

*Neoperla costana* Navas, 1924:72. Holo- type ♂, Costa Rica (MNHN).

**Adult habitus.**—Head yellow with dif- fuse yellow brown over ocelli; lappets brown. Median pronotal stripe pale, irreg-



Figs. 21-25. *A. blanda* structures. 21. Head and pronotum. 22. Male sternum 9. 23. Aedeagus, lateral. 24. Aedeagus, dorsal. 25. Aedeagus, ventral. Scales: 0.6 mm (21), 0.3 mm (22), 0.15 mm (23-25).

**26****27****28****29****30**

Figs. 26-30. *A. costana* structures. 26. Head and pronotum. 27. Male sternum 9. 28. Aedeagus, lateral. 29. Aedeagus, dorsal. 30. Aedeagus, ventral. Scales: 0.6 mm (26), 0.3 mm (27), 0.15 mm (28-30).

ular midlateral stripes brown, margins pale (Fig. 26). Wings transparent, veins brown.

**Male.**—Forewing length 8.5 mm. Hammer thimble shaped, height greater than diameter (Fig. 27). Aedeagal apex simple, scoop shaped; dorsal keel weak, hooks slender (Figs. 28–30).

**Female.**—Unknown.

**Nymph.**—Unknown.

**Material.**—Costa Rica: Puntarenas: Rio Guineal, ca. 1 km E Finca Helechales, 840 m, 22 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 1 ♂ (BPS). Rio Singri, ca. 2 km S Finca Helechales, 22 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 2 ♂ (UMSP, INBIO).

**Comments.**—*Anacroneuria costana* is a member of a large and difficult species complex found throughout Central and South America. Among Costa Rican species, *A. costana* most closely resembles *A. marginata*, new species, but that species has a shorter and more robust aedeagal apex. The aedeagus of these Puntarenas males closely resembles the figures of the holotype provided by L. Benedetto (L. Benedetto, pers. comm.).

*Anacroneuria curiosa*, new species

Figs. 31–35, 165–166

*Anacroneuria flavominuta*: Harper, 1992: 116.

**Adult habitus.**—Head yellow except for lappets. Pronotum with irregular dark lateral bands and a wide mesal yellow band (Fig. 31). Femora yellow with narrow black apical band. Wing membrane and most veins brown; R vein dark brown, C pale.

**Male.**—Forewing length 8–9 mm. Hammer thimble shaped, height greater than diameter (Fig. 32). Dorsal aspect of aedeagal apex trilobed; mesal lobe longer than lateral lobes and weakly keeled basally (Figs. 33–35, 165–166). Apex offset from dorsal sclerite by prominent transverse fold (Fig. 165).

**Female.**—Unknown.

**Nymph.**—Unknown.

**Etymology.**—The species name, meaning inquisitive or curious, alludes to the peculiar transverse dorsal fold on the aedeagal apex whose function will require even greater curiosity to discern.

**Types.**—Holotype ♂ and 15 ♂ paratypes from Costa Rica, Guanacaste, Parque Nacional Guanacaste, Maritza, Rio Tempisque, 550 m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal (USNM). Additional Paratypes: Costa Rica: Alajuela: Rio Bochinche tributary, Cerro Campana, 6 km NW Dos Rios, 600 m, 22 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 3 ♂ (UMSP). Guanacaste: Quebrada Garcia, 470 m, 8 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (BPS). Parque Nacional Guanacaste, Estacion Pitilla, Rio Orosi, 700 m, 19 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 2 ♂ (USNM). Parque Nacional Guanacaste, Estacion Maritza, Rio Tempisque, 550 m, 30 Aug 1990, J. Huisman, R. Blahnik, F. Quesada, 1 ♂ (UMSP). Estacion Maritza, Rio Tempisque, 25 May 1990, 1 ♂ (SWRC). Same location, 30 May 1990, 1 ♂ (INBIO). Nicaragua: Pte. Quinama, E Villa Somoza, 29 Jul 1967, O. S. Flint, 1 ♂ (USNM).

**Diagnosis.**—This species resembles *A. uatsi* in size and general coloration but the two are quite distinct in aedeagal features. In dorsal aspect *A. curiosa* has a complete transverse fold (Fig. 34) whereas *A. uatsi* has only a minute keel (Fig. 114).

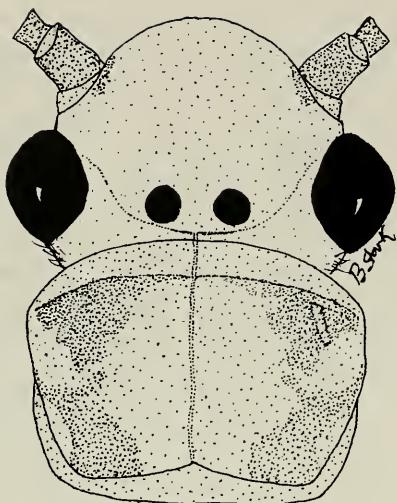
**Comments.**—This small species ranges at least from Panama to Nicaragua but may be uncommon. Harper's (1992) figure of the aedeagus of an *A. flavominuta* paratype from Panama is typical of this species and distinct from the allotype male of *A. flavominuta* from Mexico.

*Anacroneuria divisa* (Navas)

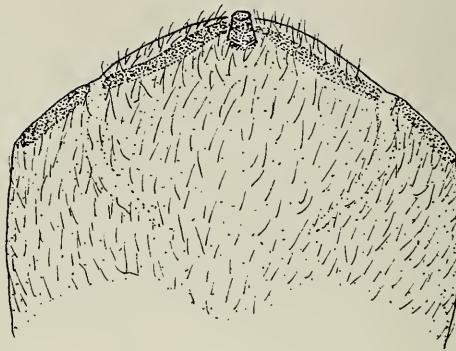
Figs. 36–40, 141, 167–168

*Forquilla divisa* Navas 1924:74. Syntype ♀, Costa Rica (NMNH).

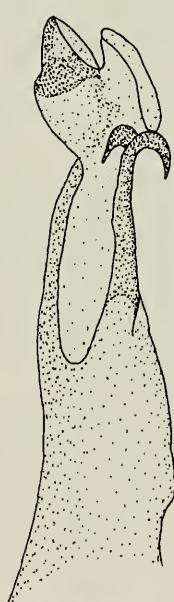
**Adult habitus.**—Head with dark pattern over ocelli extending onto clypeus, but interrupted by pale M-line; pale oval areas



31

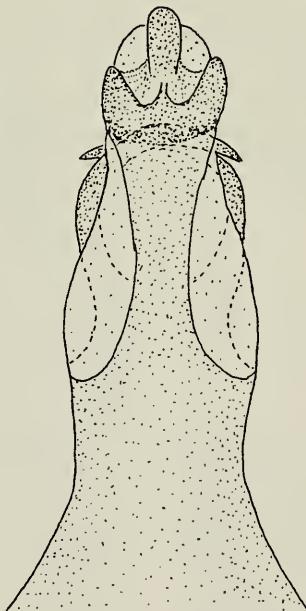


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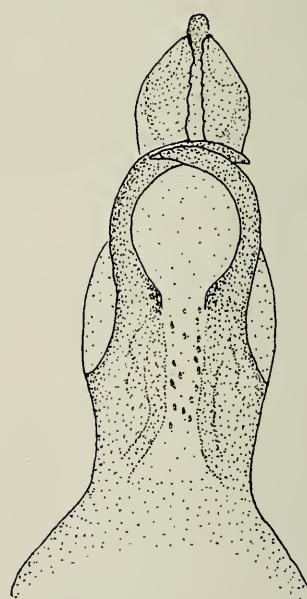


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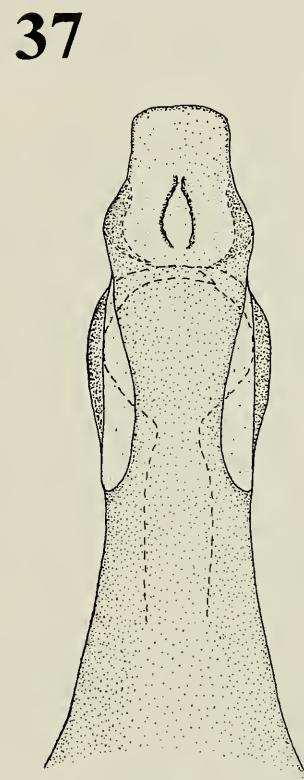
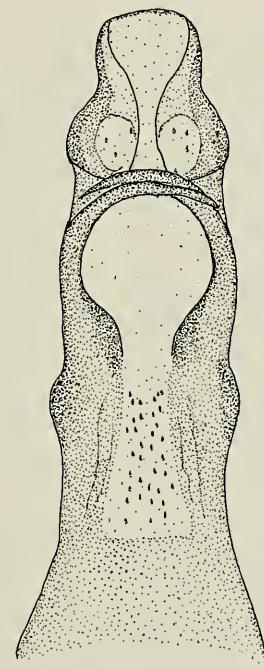
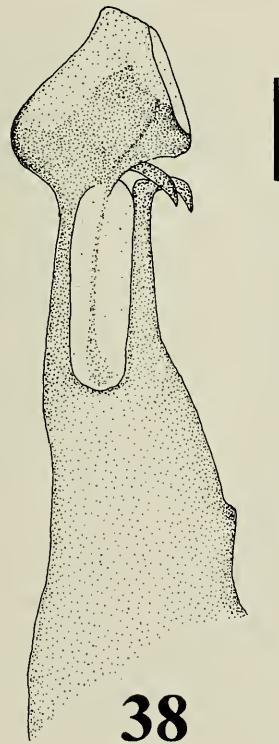
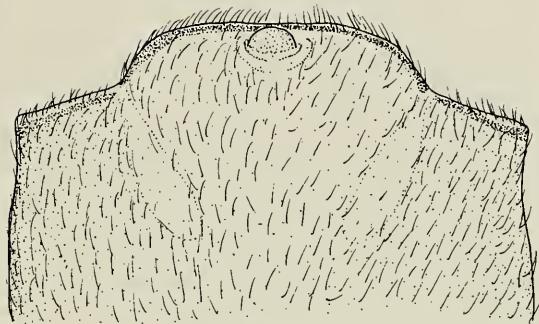
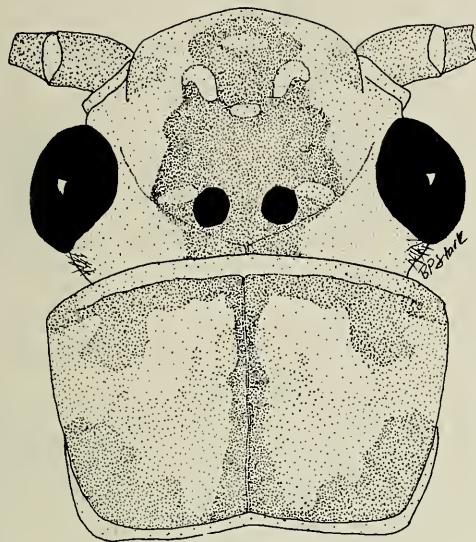


34



35

Figs. 31-35. *A. curiosa* structures. 31. Head and pronotum. 32. Male sternum 9. 33. Aedeagus, lateral. 34. Aedeagus, dorsal. 35. Aedeagus, ventral. Scales: 0.6 mm (31), 0.3 mm (32), 0.15 mm (33-35).



Figs. 36-40. *A. divisa* structures. 36. Head and pronotum. 37. Male sternum 9. 38. Aedeagus, lateral. 39. Aedeagus, ventral. 40. Aedeagus, dorsal. Scales: 0.6 mm (36), 0.3 mm (37), 0.15 mm (38-40).

lateral to ocelli and minute spots anterolateral to ocelli, lappets diffuse brown. Median pronotal stripe brown; anterior and posterior margins brown, disc and anterolateral margins pale (Fig. 36). Wing membrane brown, veins C, Sc and R pale, other veins brown.

**Male.**—Forewing length 13–15 mm. Hammer low, nipple shaped (Fig. 37). Aedeagal apex simple, scoop shaped with broad, rounded shoulders. Lateral aspect expanded through dorsal keel; hooks slender (Figs. 38–40, 167–168).

**Female.**—Forewing length 17–19 mm. Subgenital plate four lobed; lateral lobes larger than median lobes. Transverse sclerite of sternum nine with median notch; median sclerite T-shaped, lateral setae prominent (Fig. 141).

**Nymph.**—Unknown.

**Material.**—Costa Rica: Alajuela: Cerro Campana, Rio Bochinche tributary, 6 km NW Dos Ríos, 600 m, 22 Jul 1987, R. Holzenthal, J. Morse, P. Clausen 12 ♂, 3 ♀ (UMSP, INBIO). Rio Peje, 1 km SE San Vicente, 1450 m, 14 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 4 ♀ (INBIO). Reserva Forestal San Ramon, Rio San Lorcencito, 980 m, 30 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (UMSP). Guanacaste: Parque Nacional Guanacaste, Maritza, Rio Tempisque, 550 m, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 12 ♂ (BPS, INBIO, UMSP). Estacion Maritza, Rio Tempisque, 11 Feb 1990, 2 ♂ (SWRC). Same location, 17 Mar 1989, 1 ♂, 1 ♀ (BPS). Same location, 11 Apr 1990, 10 ♂ (SWRC). Same location, 28 May 1989, 4 ♂, 1 ♀ (INBIO). Same location, 22 Oct 1990, 6 ♂, 1 ♀ (SWRC). Same location, 11 Nov 1989, 1 ♂, 1 ♀ (BPS). Parque Nacional Guanacaste, Rio San Josecito, Estacion Mengo, 960 m, 28 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 2 ♂ (UMSP). Parque Nacional Guanacaste, Rio Orosi, Estacion Pitilla, 700 m, 22 May 1990, R. Holzenthal, R. Blahnik, 14 ♂, 5 ♀ (BPS, UMSP). Parque Nacional Guanacaste, El Hacha, Quebrada Alcornoque, 250 m, 26

Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂ (UMSP). Parque Nacional Rincon de la Vieja, Quebrada Zapilote, 785 m, 3 Mar 1986, R. Holzenthal, 1 ♂ (BPS). Quebrada Garcia, 470 m, 8 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (BPS).

**Comments.**—The male syntype is missing but L. Benedetto provided notes on the female syntype.

*Anacroneuria exquisita*, new species

Figs. 41–45

**Adult habitus.**—Head yellow. Median pronotal stripe broad and pale; irregular lateral stripes brown, margins pale (Fig. 41). Wings pale amber, transparent circular window beyond cord; veins C, Sc and R pale, others brown.

**Male.**—Forewing length 14 mm. Hammer a low membranous disc (Fig. 42). Aedeagal apex trilobed, lateral lobes small and covered ventrally by membranous processes. Dorsal keel inconspicuous, hooks slender (Figs. 43–45).

**Female.**—Unknown.

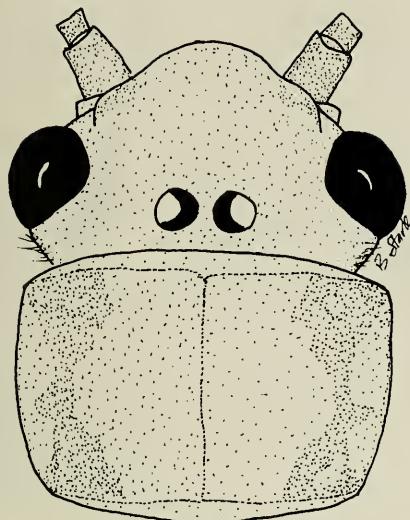
**Nymph.**—Unknown.

**Etymology.**—The species name, meaning excellent or admirable, refers to the distinctive adult color pattern.

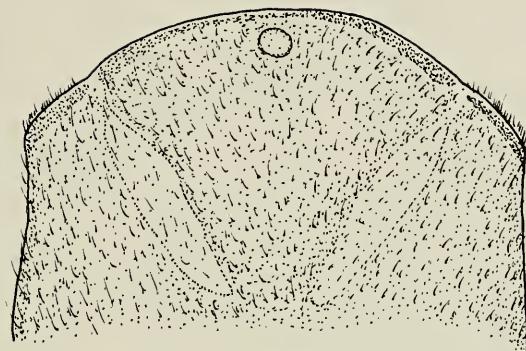
**Types.**—Holotype ♂ (USNM) and four ♂ paratypes (BPS, UMSP) from Costa Rica, San Jose, Parque Nacional Braulio Carrillo, Rio Zurqui, 1650 m, 6 Jul 1986, R. Holzenthal, M. Heyn, B. Armitage.

**Diagnosis.**—*A. exquisita* is similar in aedeagal features to *A. perplexa* (Figs. 88–90) but that species is smaller and darker (Fig. 86). *A. ventana* has a similar wing pattern but differs in aedeagal structure (Figs. 124–125), hammer shape (Fig. 122) and head pattern (Fig. 121).

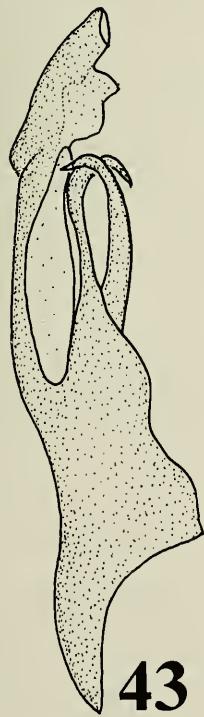
A series of female specimens from Estacion Maritza are similar in color pattern but they are smaller, have a dark ocellar patch and the dark pronotal stripes are larger and convergent posteriorly. Thus these specimens remain unassociated and the female of *A. exquisita*, unknown.



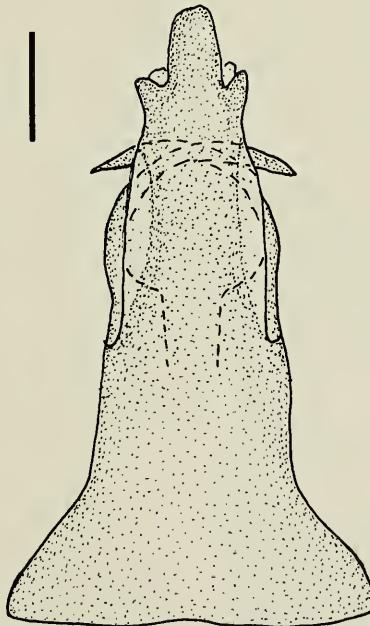
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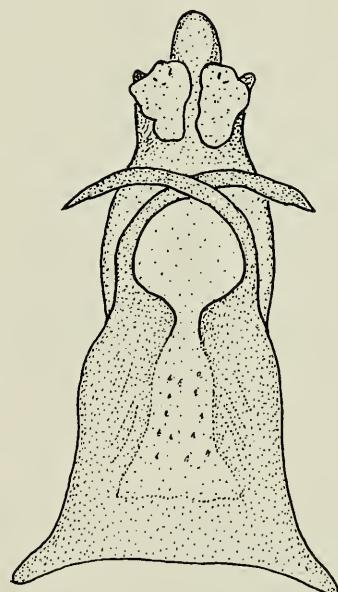
42



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44



45

Figs. 41-45. *A. exquisita* structures. 41. Head and pronotum. 42. Male sternum 9. 43. Aedeagus, lateral. 44. Aedeagus, dorsal. 45. Aedeagus, ventral. Scales: 0.6 mm (41), 0.3 mm (42), 0.15 mm (43-45).

*Anacroneuria hacha*, new species

Figs. 48–50, 169–170

**Adult habitus.**—Dark head pattern covers ocelli and extends to anterior margin; pattern diffuse and almost interrupted at M-line. Median pronotal stripe diffuse brown, bordered by yellow; irregular midlateral stripes brown, margins pale (Fig. 46). Wing membrane brown, veins brown.

**Male.**—Forewing length 10–11 mm. Hammer a low indistinct mound (Fig. 47). Aedeagal apex simple, dorsal margin truncate or emarginate, keel well developed. Lateral aspect somewhat hatchet shaped; hooks slender (Fig. 48–50, 169–170).

**Female.**—Unknown.

**Nymph.**—Unknown.

**Etymology.**—Hacha, Spanish for axe, referring to the hatchet shaped aedeagal apex, is used as a noun in apposition.

**Types.**—Holotype ♂ (USNM) and 1 ♂ paratype (SWRC) from Costa Rica, Guanacaste, Estacion Maritza, Rio Tempisque, 27 Apr 1989. Additional Paratypes: Costa Roca: Type locality, 11 May 1990, 2 ♂ (SWRC). Same location, 21 May 1990, 1 ♂ (SWRC). Same location, 30 May 1990, 6 ♂ (BPS). Same location, 10 Oct 1989, 1 ♂ (SWRC). Same location, 22 Oct 1990, 4 ♂ (INBIO). Parque Nacional Guanacaste Maritza, Rio Tempisque, 550 m, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 6 ♂ (UMSP). Same location, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 10 ♂ (USNM).

**Diagnosis.**—*A. hacha* is similar to *A. divisa* in color pattern (Fig. 36) and general aedeagal shape (Figs. 38–40), but the two are distinguished on the basis of the hammer (Figs. 37, 47) and aedeagal keel (Figs. 40, 49).

*Anacroneuria harperi*, new species

Figs. 51–55, 142

*Anacroneuria* sp. B: Harper, 1992:118.

**Adult habitus.**—Head yellow with diffuse brown area forward of ocelli; lappets

brown. Median pronotal stripe yellow; most of disc pale brown, anterolateral margins pale (Fig. 51). Wing membrane brown, veins brown.

**Male.**—Forewing length 7 mm. Hammer thimble shaped, height greater than diameter (Fig. 52). Aedeagal body asymmetrical, apex twisted in a slight sinistral direction. Hooks twisted and asymmetrical; apex of right hook recurved. Dorsal keel absent (Figs. 53–55).

**Female.**—Forewing length 9 mm. Subgenital plate four lobed; inner lobes smaller than outer lobes. Transverse sclerite of sternum nine narrow; mesal area of sclerite densely setose. Mesal sclerite T-shaped, lateral setae prominent (Fig. 142).

**Nymph.**—Unknown.

**Etymology.**—The patronym honors P. Harper for his recognition of this interesting species.

**Types.**—Holotype ♂ from Panama, Alajuela, 17 Apr 1911, A. Busck (USNM). Paratypes: Panama: Alajuela: 6 Apr 1911, A. Busck, 1 ♂, 1 ♀ (USNM). Same location, 16 Apr 1911, A. Busck, 1 ♂ (USNM). Same location, 8 Mar 1912, A. Busck, 1 ♀ (USNM). Darien Province: Santa Fe, 28 May 1967, D. M. Delong, C. A. Triplehorn, 1 ♂ (OSU).

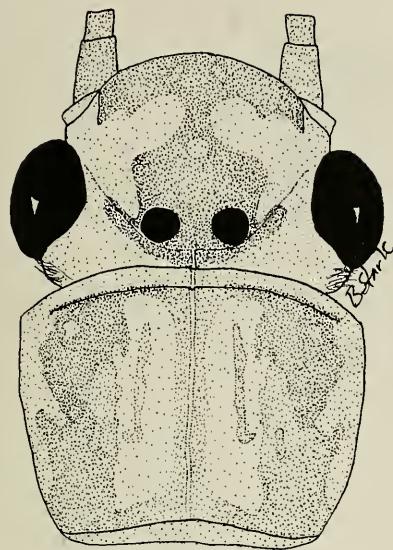
**Diagnosis.**—In size and general coloration this species is similar to *A. curiosa* and *A. uatsi* but the twisted aedeagal apex (Figs. 53–55) is unique to this species.

*Anacroneuria holzenthalii*, new species

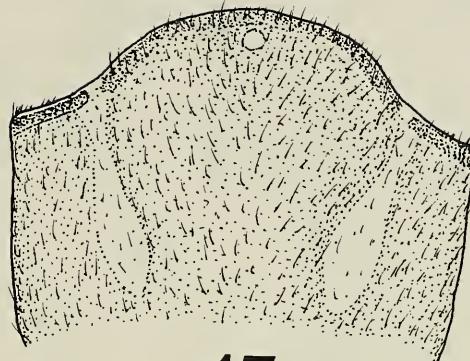
Figs. 56–60, 143, 171–172

**Adult habitus.**—Dark pattern covers ocelli and extends forward to midpoint of lappets; pattern interrupted by a pair of minute pore sized unpigmented spots and a larger mesal spot. Pronotum dark except for slender mesal stripe and anterolateral marginal spots (Fig. 56). Wing membrane brown, veins brown.

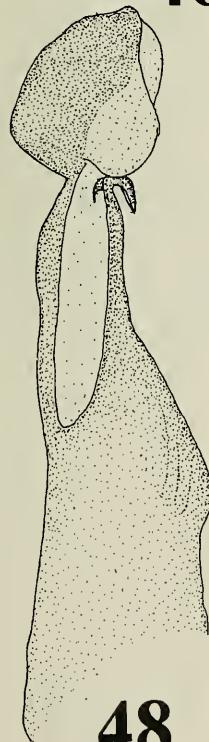
**Male.**—Forewing length 10–12 mm. Hammer thimble shaped (Fig. 57). Aedeagal apex multilobed, shoulders winged.



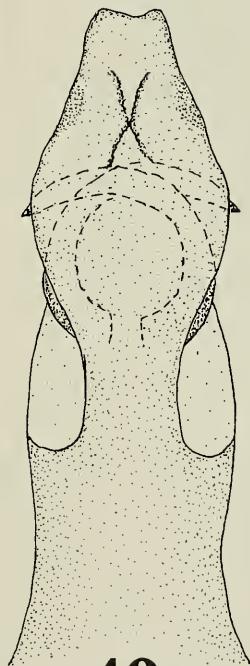
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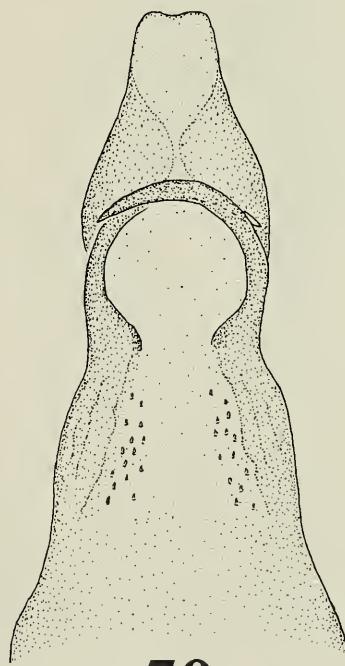
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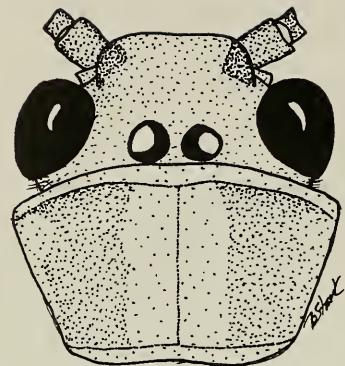


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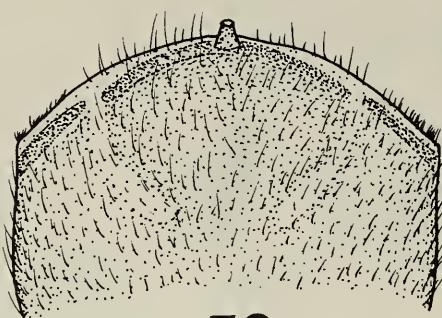


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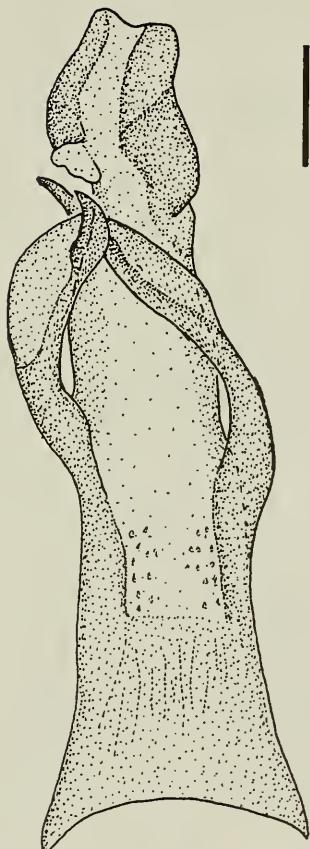
Figs. 46-50. *A. hacha* structures. 46. Head and pronotum. 47. Male sternum 9. 48. Aedeagus, lateral. 49. Aedeagus, dorsal. 50. Aedeagus, ventral. Scales: 0.6 mm (46), 0.3 mm (47), 0.15 mm (48-50).



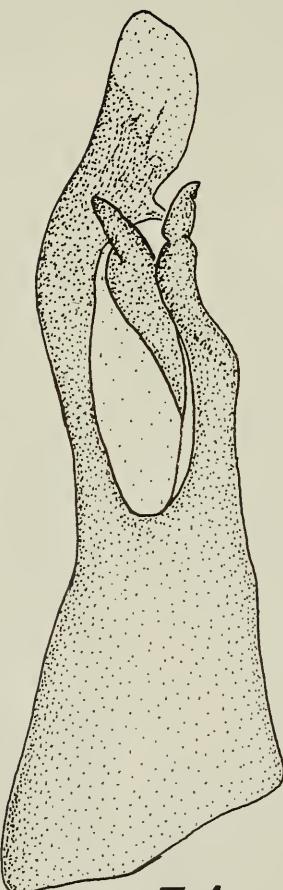
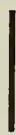
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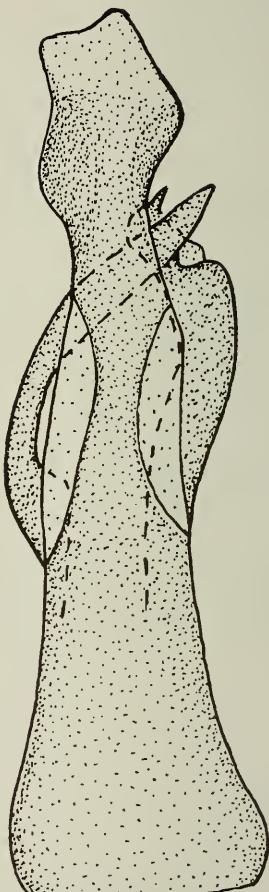
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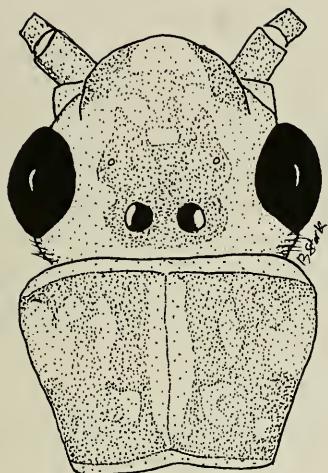


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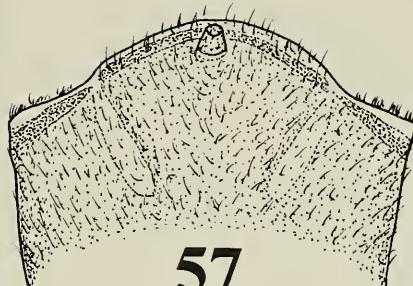


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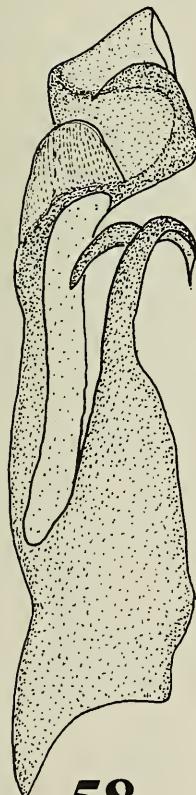
Figs. 51-55. *A. harperi* structures. 51. Head and pronotum. 52. Male sternum 9. 53. Aedeagus, ventral. 54. Aedeagus, lateral. 55. Aedeagus, dorsal. Scales: 0.6 mm (51), 0.3 mm (52), 0.15 mm (53-55).



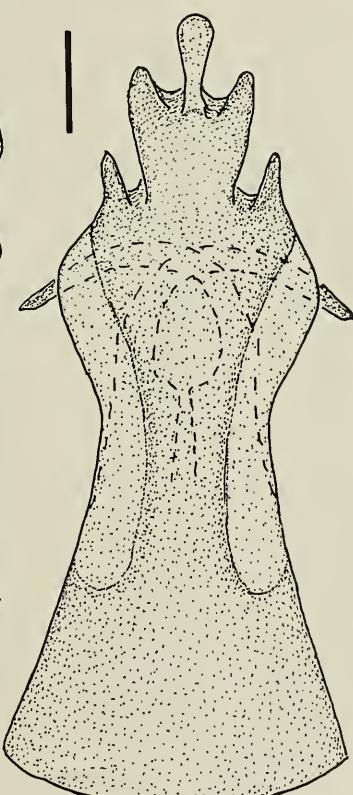
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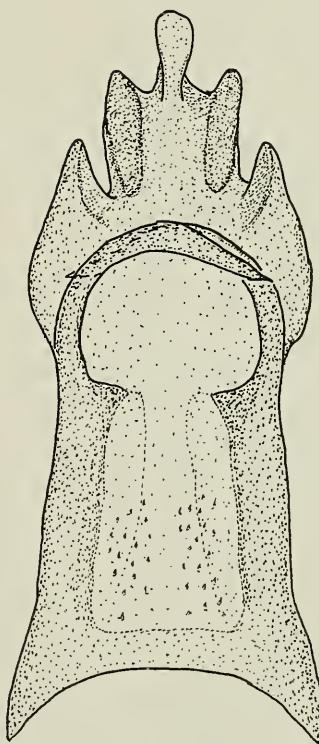
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58



59



60

Figs. 56-60. *A. holzenthalii* structures. 56. Head and pronotum. 57. Male sternum 9. 58. Aedeagus, lateral. 59. Aedeagus, dorsal. 60. Aedeagus, ventral. Scales: 0.6 mm (56), 0.3 mm (57), 0.15 mm (58-60).

Dorsal keel transverse, hooks slender (Figs. 58–60, 171–172).

*Female*.—Forewing length 14–15 mm. Subgenital plate four lobed; mesal notch deep, V-shaped, lateral notches shallow. Transverse sclerite of sternum nine sinuate, mesal sclerite T-shaped and setose. Setae on sclerite stalk minute, lateral setae prominent (Fig. 143).

*Nymph*.—Unknown.

*Etymology*.—The patronym honors R. W. Holzenthal for his outstanding contributions to our understanding of the Costa Rican aquatic insect fauna.

*Types*.—Holotype ♂ from Costa Rica, Guanacaste, Parque Nacional Rincon de la Vieja, Quebrada Zapilote, 785 m, 3 Mar 1986, R. Holzenthal (USNM). Paratypes: Costa Rica: Alajuela, Reserva Forestal San Ramon, Rio San Lorencito, 980 m, 6–10 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 6 ♂, 11 ♀ (INBIO, UMSP). Guanacaste: Quebrada Garcia, 10.6 km ENE Quebrada Grande, 470 m, 8 Mar 1986, R. Holzenthal, W. Fasth, 3 ♂ (UMSP). Guanacaste, Parque Nacional Guanacaste, Maritza, Rio Tempisque, 550 m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 4 ♂, 1 ♀ (USNM). Same location, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 2 ♂ (UMSP). Parque Nacional Guanacaste, Rio Tempisque Sur, Maritza, 600 m, 30 Aug 1990, J. Huisman, F. Quesada, 1 ♂, 1 ♀ (BPS). Estacion Maritza, Rio Tempisque, 11 May 1990, 2 ♂ (SWRC). Same location, 17 Mar 1989, 1 ♂, 1 ♀ mating (SWRC). Same location, 28 Apr 1989, 1 ♂, 1 ♀ (SWRC). Heredia: Quebrada Chiquiza, Rava Avis Biological Station, 550 m, 31 Mar 1989, R. Blahnik, Solis 1 ♂ (UMSP). Nicaragua: Chontales, Santo Domingo, Nov 1985, J. M. Maes, 1 ♂ (USNM).

*Diagnosis*.—See under *A. benedettoi*.

*Anacroneuria lineata* (Navas)  
Figs. 61–65

*Neoperla lineata* Navas, 1924:73. Holotype ♂, Costa Rica (MNHN).

*Adult habitus*.—Head with dark pattern over ocelli extending to M-line; lappets and small triangular patch forward of M-line dark. Median pronotal stripe diffuse brown, bordered by yellow; margins dark (Fig. 61). Wing membrane transparent, veins brown.

*Male*.—Forewing length 12 mm. Hammer nipple shaped (Fig. 62). Aedeagal apex broad, scoop shaped with a pair of small lateral projections at shoulder. Dorsal keel prominent, hooks slender (Figs. 63–65).

*Female*.—Unknown.

*Nymph*.—Unknown.

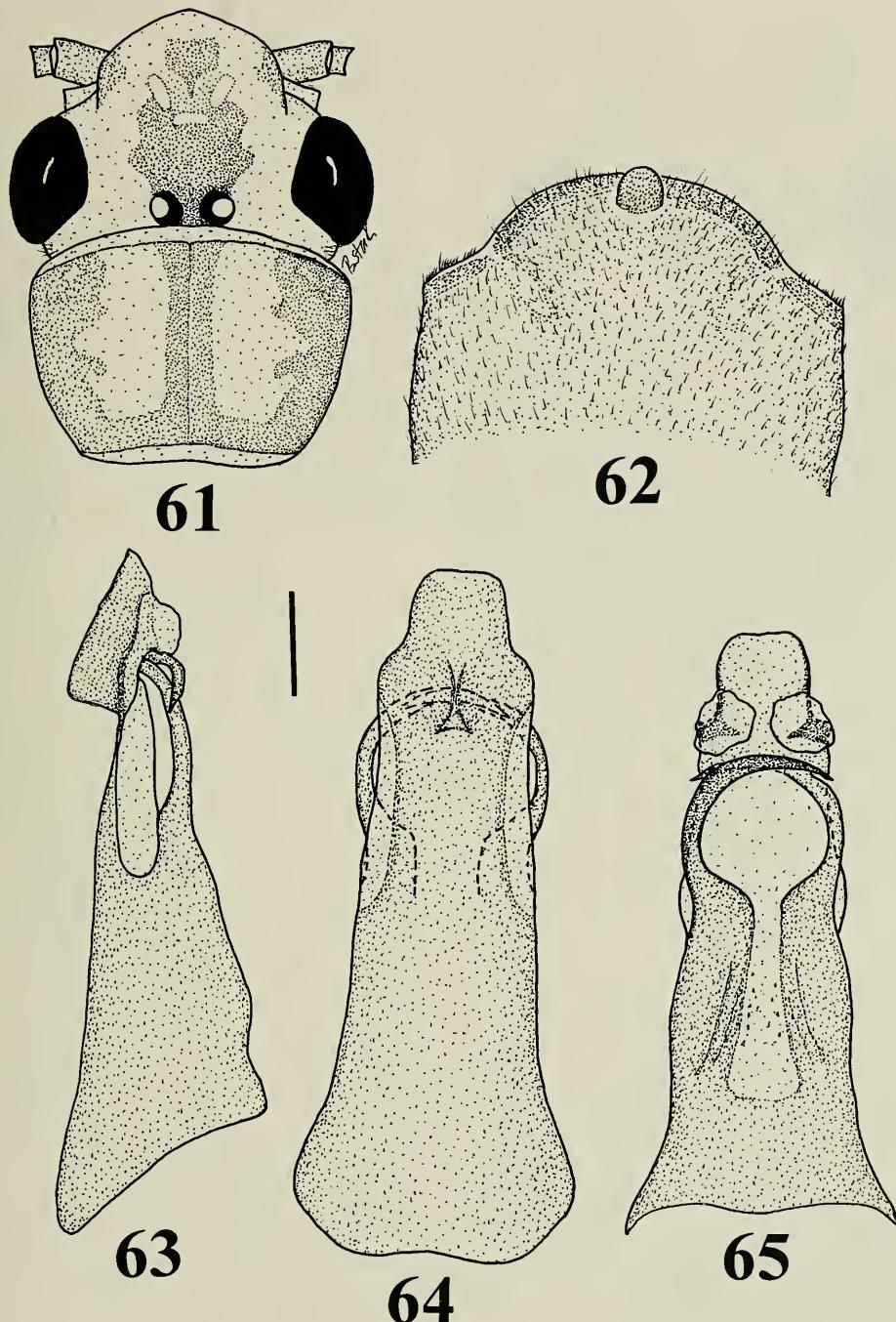
*Material*.—Costa Rica: Alajuela: Rio Pizote, ca. 5 km N Dos Rios, 470 m, 9 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (UMSP). Parque nacional Rincon de la Vieja, Quebrada Provision, 810 m, 4 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (UMSP). Guanacaste: Rio Mena, 4.2 km W Santa Cecilia, 11 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (UMSP). Parque Nacional Guanacaste, Maritza, Rio Tempisque, 550 m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 3 ♂ (USNM). Estacion Maritza, Rio Tempisque, 10 Oct 1989, 1 ♂ (SWRC). Same location, 11 Apr 1990, 1 ♂ (SWRC). Same location, 11 May 1990, 2 ♂ (INBIO). Rio Gongora, 4 km NE Quebrada Grande, 590 m, 21 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 10 ♂ (UMSP, BPS). San Jose: Palmital de Guarco, Cerro de la Muerte, km 37 Pan American Highway, 7 May 1995, R. W. Baumann, B. Houseman, 1 ♂ (BYU). MEXICO: Chiapas: 10 mi N Palenque, 14 June 1971, J. Zimmerman, 6 ♂, 5 ♀ (BPS).

*Comments*.—Figures of the holotype aedeagus provided by L. Benedetto seem to match this species.

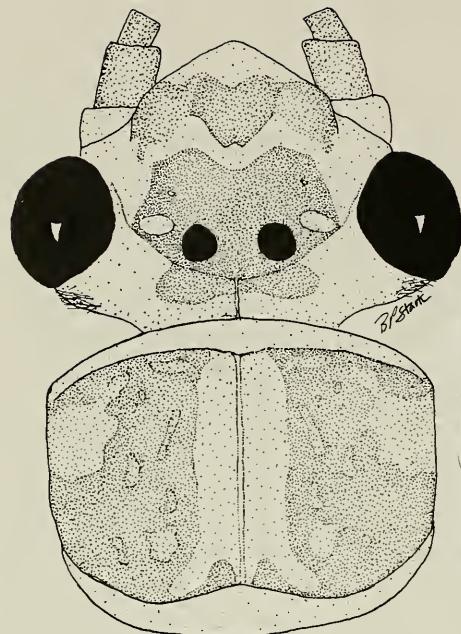
*Anacroneuria magnirufa* Jewett  
Figs. 66–70, 144, 155, 173–174

*Anacroneuria magnirufa* Jewett, 1958:162.  
Holotype ♀, El Volcan, Chiriqui, Panama (AMNH).

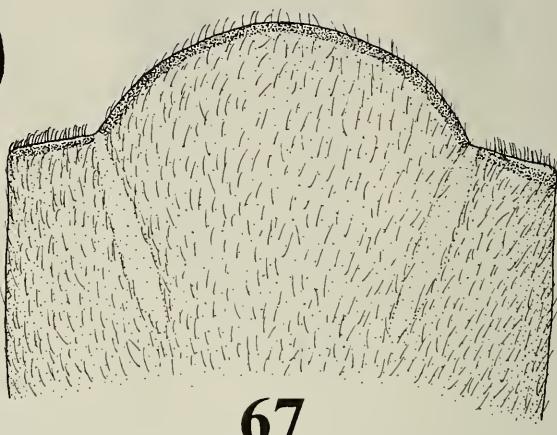
*Adult habitus*.—Dark brown pigment extends from behind ocelli to M-line; lateral



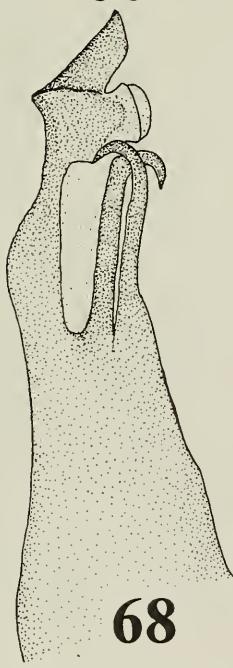
Figs. 61-65. *A. lineata* structures. 61. Head and pronotum. 62. Male sternum 9. 63. Aedeagus, lateral. 64. Aedeagus, dorsal. 65. Aedeagus, ventral. Scales: 0.6 mm (61), 0.3 mm (62), 0.15 mm (63-65).



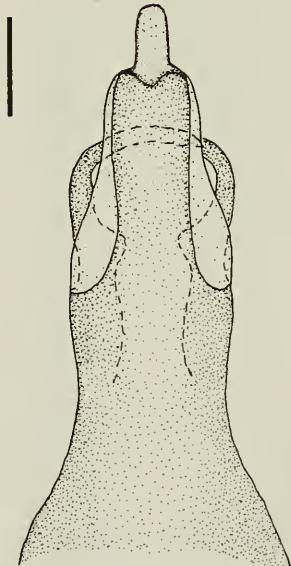
66



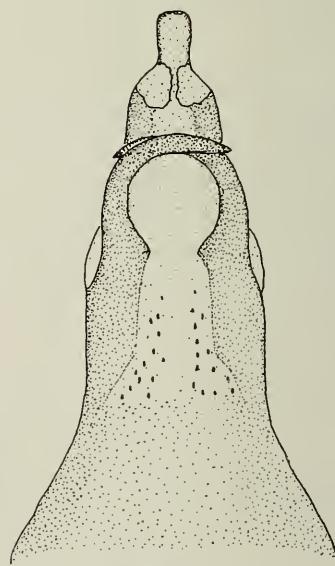
67



68



69



70

Figs. 66-70. *A. magnirufa* structures. 66. Head and pronotum. 67. Male sternum 9. 68. Aedeagus, lateral. 69. Aedeagus, dorsal. 70. Aedeagus, ventral. Scales: 0.6 mm (66), 0.3 mm (67), 0.15 mm (68-70).

callosities prominent; lappets and mesal field forward of M-line dark brown. Pronotum brown except for scattered pale rugosities and a narrow pale mesal band (Fig. 66). Wing membrane and veins dark brown.

**Male.**—Forewing length 17–20 mm. Hammer absent (Fig. 67). Aedeagal apex narrow and scoop shaped, ventral aspect with a pair of small membranous processes. Dorsal keel a thin transverse ridge, hooks slender (Figs. 68–70, 173–174).

**Female.**—Forewing length 23–26 mm. Subgenital plate bilobed, margins truncate or slightly rounded. Mesal notch shallow, small longitudinal tubercle forward of notch. Transverse sclerite absent from sternum nine, mesal sclerite sparsely setose (Fig. 144).

**Nymph.**—Unknown.

**Material.**—Costa Rica: Alajuela: Rio Peje, 1 km SE San Vicente, 1450 m, 15 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 26 ♂, 15 ♀ (BPS, INBIO, UMSP). Rio Pizote, 5 km S Brasilia, 390 m, 12 Mar 1986, R. Holzenthal, W. Fasth, 2 ♂ (UMSP). Rio Bochinche, Cerro Campana, 600 m, 22 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂ (UMSP). Rio San Lorencito, Reserva Forestal San Ramon, 980 m, 1 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂, 2 ♀. Same location, 6–10 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 3 ♂ (BPS). Guanacaste: Rio Los Ahogados, 11.3 km ENE Quebrada Grande, 470 m, 7 Mar 1986, R. Holzenthal, W. Fasth, 2 ♂, 1 ♀ (UMSP). Rio Gongora, 590 m, 21 Aug 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂, 1 ♀ (UMSP). Estacion Maritza, Rio Tempisque, 14 Jan 1990, 1 ♂ (SWRC). Same location, 11 Feb 1990, 1 ♂ (SWRC). Same location, 11 Apr 1990, 1 ♂ (SWRC). Same location, 28 Apr 1989, 1 ♂, 3 ♀ (SWRC). Same location, 11 May 1990, 1 ♂ (SWRC). Same location, 30 May 1990, 1 ♂ (SWRC). Same location, 5 Jul 1989, 1 ♀ (SWRC). Same location, 19 Aug 1989, 2 ♂, 2 ♀ (SWRC). Same location, 10 Oct 1989, 2 ♂, 1 ♀ (SWRC). Same location, 11 Nov 1989, 1 ♂ (SWRC). Puntarenas: Rio

Bellavista, ca. 1.5 km NW Las Alturas, 1400 m, 10 Aug 1990, R. Holzenthal, R. Blahnik, F. Munoz, 2 ♂ (UMSP). Same location, 16 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 3 ♂ (BPS). Panama: Chiriqui, Guadalupe Arriba, 11–17 Sep 1985, H. Wolda, 2 ♂ (BYU). Same location, 10–16 Jul 1985, H. Wolda, 2 ♂ (BYU). Same location, 24–30 Jul 1985, H. Wolda, 1 ♂ (BYU).

**Comments.**—Collections of *A. magnirufa* in Costa Rica are known from throughout the year, and the known species range is from Panama to Honduras. Few specimens are available from Panama and these are larger and have a slightly wider aedeagal apex and less conspicuous dorsal keel than Costa Rican specimens. No specimens are known from Nicaragua and only two paratype males are known from Honduras. All Costa Rican female specimens have a mesal tubercle near the subgenital plate notch. This conspicuous feature was not mentioned by Jewett (1958) and is not shown in figures of the holotype made by Benedetto (L. Benedetto, pers. comm.). This variation in both male and female specimens from Chiriqui suggests the possibility that two closely related species are involved.

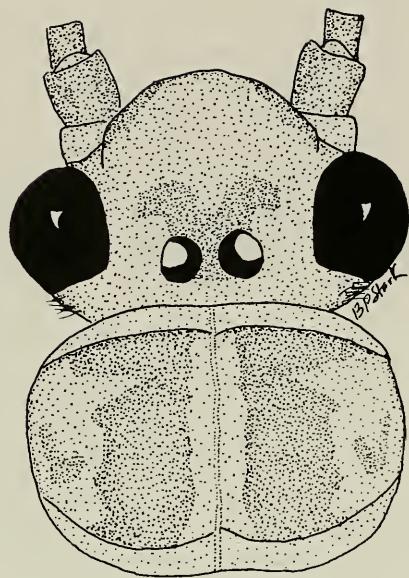
*Anacroneuria marca*, new species

Figs. 71–75, 145, 175–176

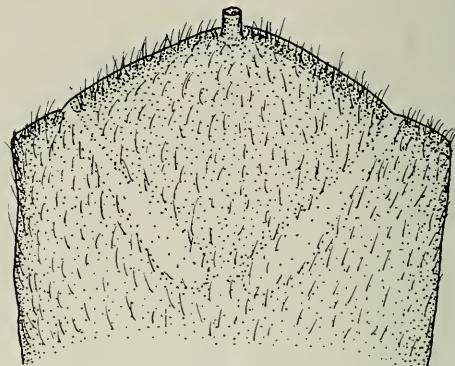
**Adult habitus.**—Head with a pair of brown L-shaped marks extending from ocelli but sometimes fused between ocelli; lappets brown. Pronotum with a narrow median yellow band; lateral area brown but with scattered pale rugosities and pale anterolateral margin (Fig. 71). Wing membrane transparent, veins brown.

**Male.**—Forewing length 16 mm. Hammer thimble shaped, height subequal to basal diameter (Fig. 72). Aedeagal apex simple, abruptly narrowed from shoulders to a slender scoop. Hooks slender, dorsal keel absent (Figs. 73–75, 175–176).

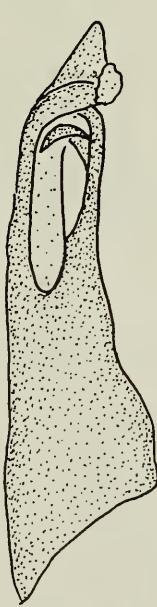
**Female.**—Forewing length 20 mm.



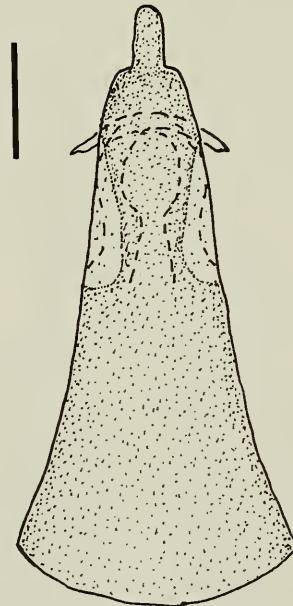
71



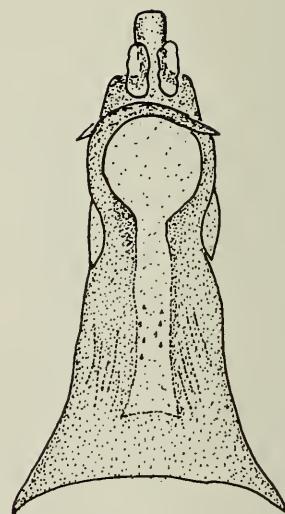
72



73

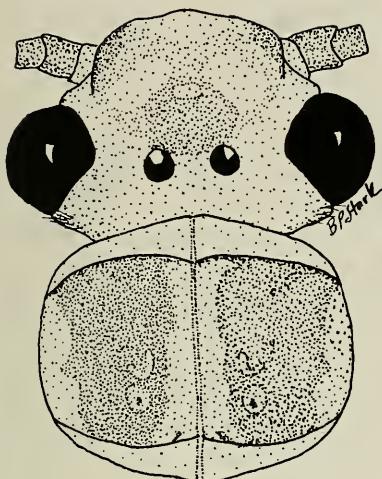


74

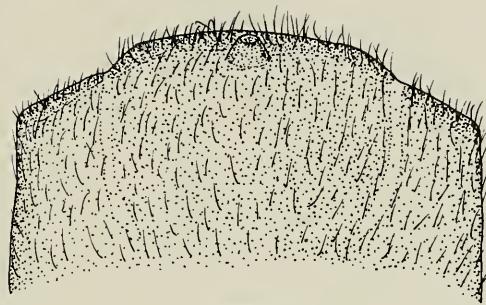


75

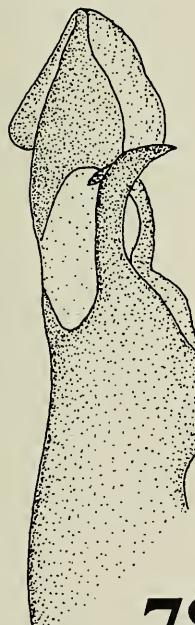
Figs. 71-75. *A. marca* structures. 71. Head and pronotum. 72. Male sternum 9. 73. Aedeagus, lateral. 74. Aedeagus, dorsal. 75. Aedeagus, ventral. Scales: 0.6 mm (71), 0.3 mm (72), 0.15 mm (73-75).



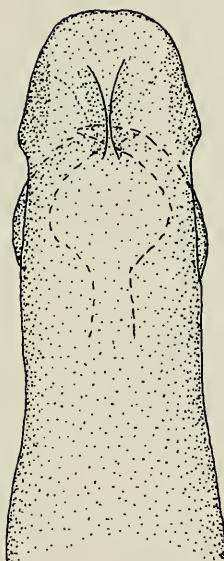
76



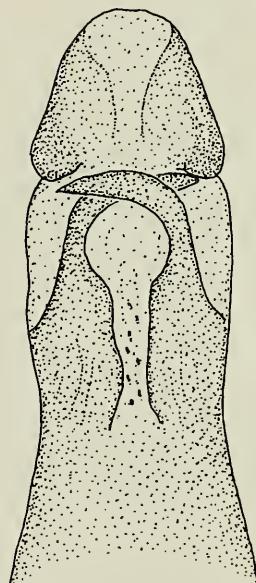
77



78



79



80

Figs. 76-80. *A. marginata* structures. 76. Head and pronotum. 77. Male sternum 9. 78. Aedeagus, lateral. 79. Aedeagus, dorsal. 80. Aedeagus, ventral. Scales: 0.6 mm (76), 0.3 mm (77), 0.15 mm (78-80).

Subgenital plate bilobed; notch V-shaped, lobes truncate to emarginate. Transverse sclerite of sternum nine wide; intersegmental membrane covered with microtri-

chia; setal patch of mesal sclerite interrupted into a median stalk and lateral setal areas (Fig. 145).

*Nymph*.—Unknown.

**Etymology.**—Marca, Spanish for brand, refers to the L-shaped marks on the head, and is used as a noun in apposition.

**Types.**—Holotype ♂ from Costa Rica, Heredia, Parque Nacional Braulio Carrillo, Rio Peje, 480 m, 29 May 1990, R. Holzenthal, R. Blahnik, F. Munoz (USNM). Paratypes: Costa Rica: Alajuela: Rio Peje, ca. 1 km SE San Vicente, 1450 m, 14 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer, 3 ♂ (UMSP). Reserva Forestal San Ramon, Rio San Lorencito, 980 m, 30 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 9 ♀ (UMSP). Same location, 6 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 3 ♀ (INBIO). Cartago: Reserva Tapanti, Rio Grande de Orosi, 1650 m, 8 Jul 1986, R. Holzenthal, M. Heyn, B. Armitage, 3 ♂, 3 ♀ (BPS). Puntarenas: Rio Coton, Las Alturas, 1360 m, 18 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 1 ♂, 1 ♀ (INBIO). Same location, 16 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 1 ♂ (BPS). Zona Protectora Las Tablas, Rio Coton, Sitio Coton, 1460 m, 15 Apr 1989, R. Holzenthal, R. Blahnik, 1 ♂, 1 ♀ (USNM). San Jose: Rio Chirripo Pacifica, 9.5 km NE Rivas, 1370 m, 23 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 1 ♀ (UMSP).

**Diagnosis.**—The color pattern of *A. marca* is similar to that of *A. ventana* (Fig. 121) but hammer shape (Fig. 122) and the aedeagal keel (Fig. 124) distinguish these species. *A. zapata* is also similar but has a trilobed aedeagal apex (Fig. 130).

*Anacroneuria marginata*, new species  
Figs. 76–80, 177–178

**Adult habitus.**—Diffuse brown pattern extends from ocelli to M-line and laterally to lappets. Pronotum with narrow pale median and marginal stripes; dark midlateral stripes rugose (Fig. 76). Wing membrane amber, veins brown.

**Male.**—Forewing length 8 mm. Hammer thimble shaped, height less than basal diameter (Fig. 77). Aedeagal apex simple, broad and rounded at tip. Dorsal keel mod-

erately developed, hooks short (Figs. 78–80, 177–178).

**Female.**—Unknown.

**Nymph.**—Unknown.

**Etymology.**—The species name, meaning bordered, refers to the pale marginal bands on the pronotum.

**Types.**—Holotype ♂ from Costa Rica, Guanacaste, Parque Nacional Guanacaste, Maritza, Rio Tempisque, 550 m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal (USNM). Paratypes: Costa Rica: Guanacaste: Parque Nacional Guanacaste, Maritza, Rio Tempisque Sur, 30 Aug 1990, 600 m, J. Huisman, F. Quesada, 1 ♂ (UMSP). Estacion Maritza, Rio Tempisque, 14 Jan 1990, 1 ♂ (SWRC). Same location, 17 Mar 1989, 1 ♂ (SWRC). Same location, 27 Apr 1989, 2 ♂ (BPS). Same location, 28 May 1989, 1 ♂ (SWRC). Same location 30 May 1990, 1 ♂ (INBIO). Same location, 22 Oct 1990, 1 ♂ (INBIO).

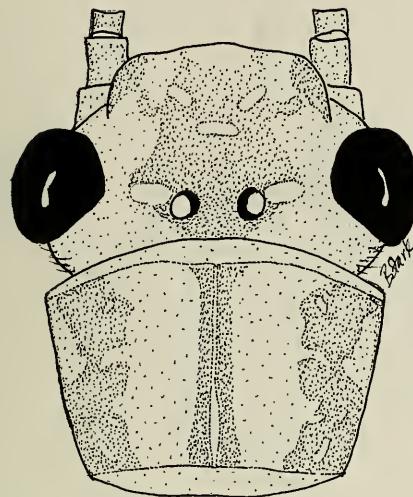
**Diagnosis.**—The aedeagus of this species is similar to that of *A. costana* (Figs. 28–30) but the apex is shorter and wider and the keel more pronounced in *A. marginata*.

*Anacroneuria maritza*, new species  
Figs. 81–85, 146, 151–152

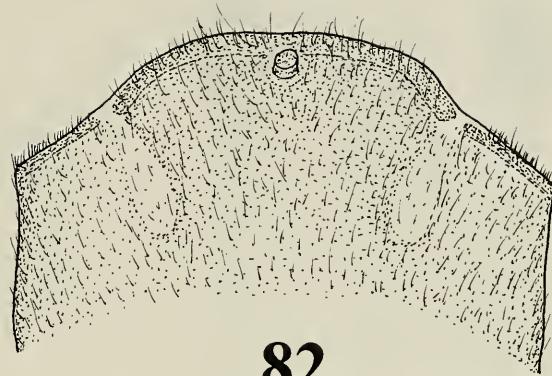
**Adult habitus.**—Dark brown covers ocelli and extends forward to M-line; lappets and a small mesal spot forward of M-line brown. Median brown pronotal stripe bordered by yellow; irregular midlateral stripes brown, margins pale (Fig. 81). Wing membrane brown, veins brown except pale C and Sc.

**Male.**—Forewing length 12–13 mm. Hammer thimble shaped, height less than basal diameter (Fig. 82). Aedeagal apex scoop shaped, tip with parallel margins and well developed dorsal keel. Ventral aspect covered with large membranous lobes; hooks slender (Figs. 83–85).

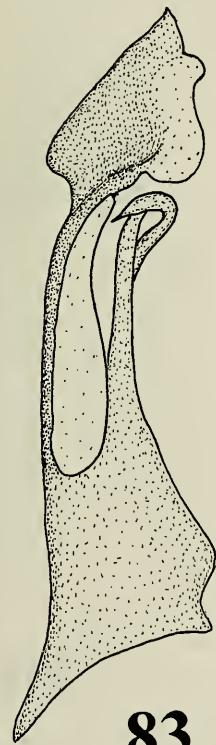
**Female.**—Forewing length 15–16 mm. Subgenital plate bilobed, notch broadly V-shaped. Transverse sclerite of sternum nine absent; mesal sclerite V-shaped and sparse-



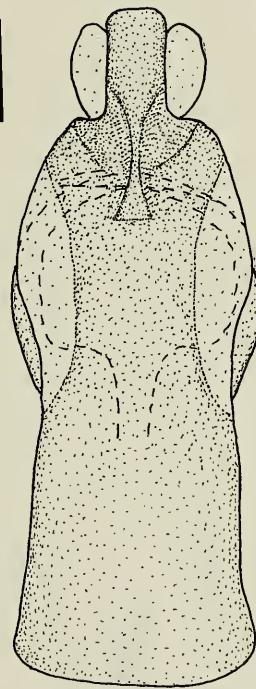
81



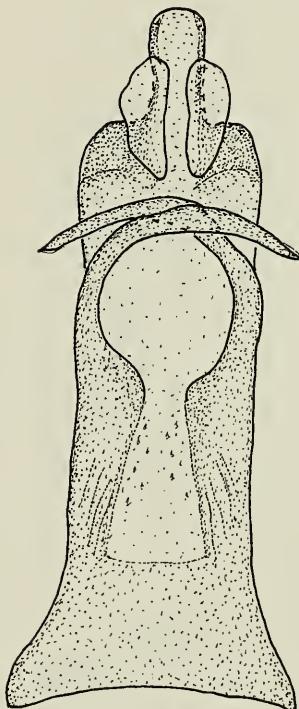
82



83

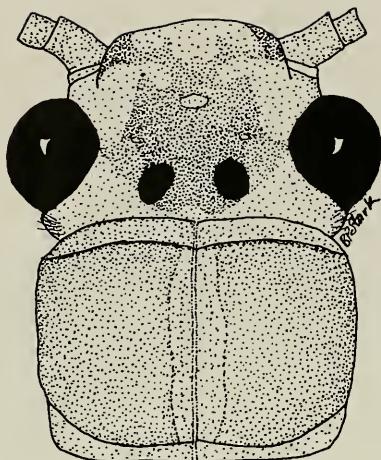


84

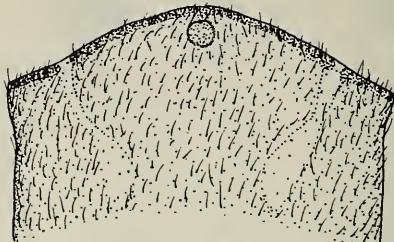


85

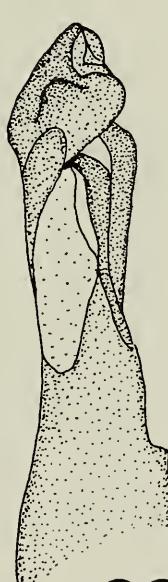
Figs. 81-85. *A. maritza* structures. 81. Head and pronotum. 82. Male sternum 9. 83. Aedeagus, lateral. 84. Aedeagus, dorsal. 85. Aedeagus, ventral. Scales: 0.6 mm (81), 0.3 mm (82), 0.15 mm (83-85).



86

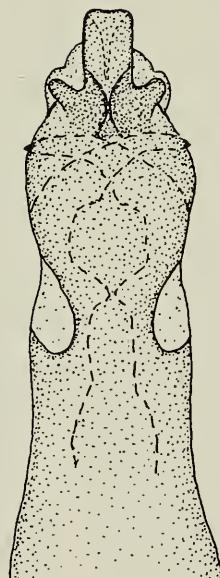


87

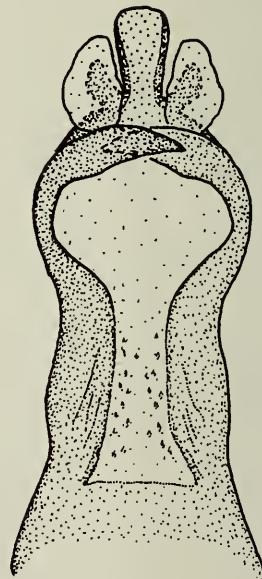


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89



90

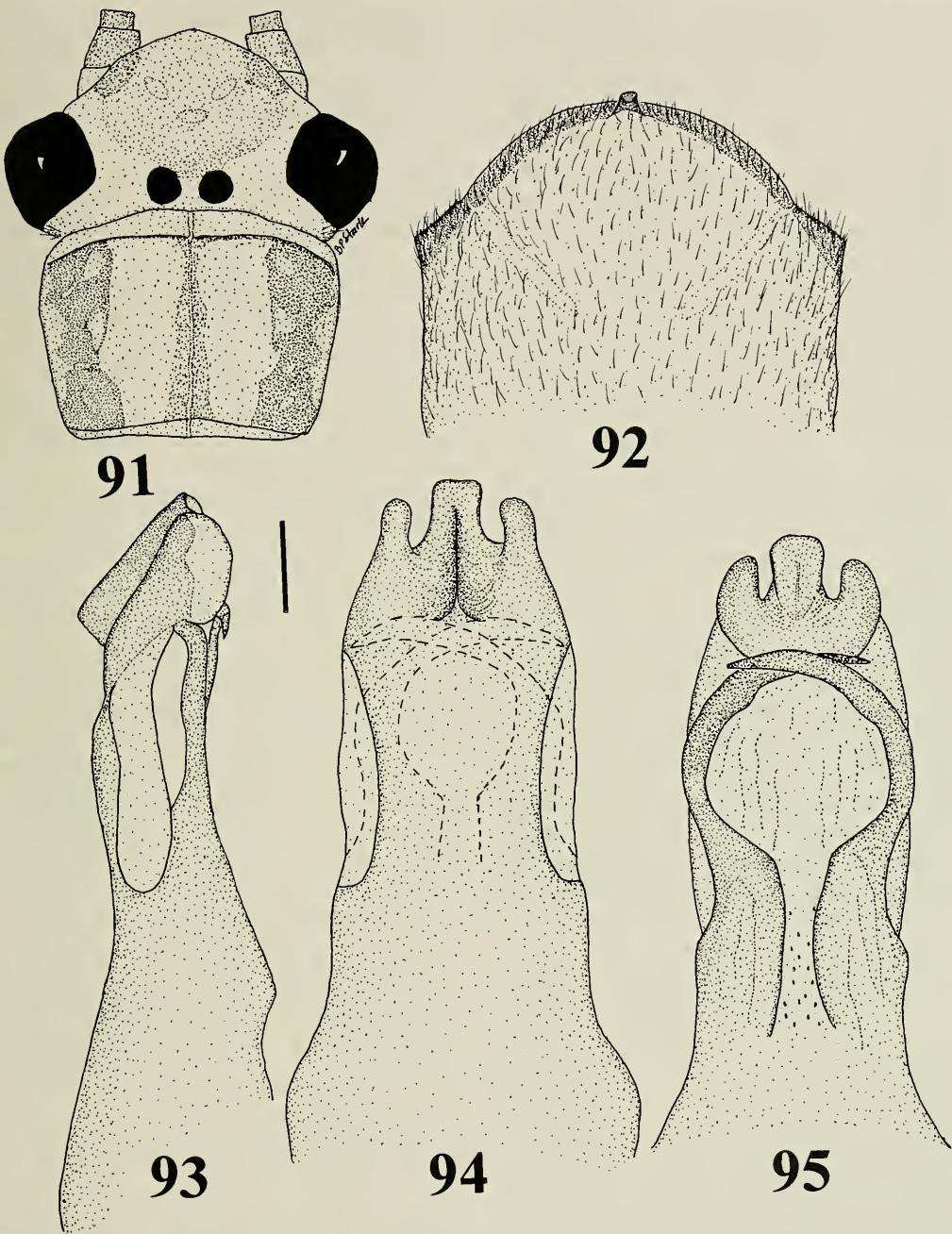
Figs. 86-90. *A. perplexa* structures. 86. Head and pronotum. 87. Male sternum. 88. Aedeagus, lateral. 89. Aedeagus, dorsal. 90. Aedeagus, ventral. Scales: 0.6 mm (86), 0.3 mm (87), 0.15 mm (88-90).

ly setose. Patch of long red-brown setae at base of lateral bar (Fig. 146).

*Nymph.*—Body length 14-17 mm. Head pattern brown except for pale M-line and

oval areas anterolateral to ocelli. Pronotum brown with scattered pale rugosities (Fig. 151).

*Etymology.*—The species name, based on



Figs. 91–95. *A. planicollis* structures. 91. Head and pronotum. 92. Male sternum 9. 93. Aedeagus, lateral. 94. Aedeagus, dorsal. 95. Aedeagus, ventral. Scales: 0.6 mm (91), 0.3 mm (92), 0.15 mm (93–95).

the type locality, is used as a noun in apposition.

*Types*.—Holotype ♂ from Costa Rica, Guanacaste, Estacion Maritza, Rio Tempis-

quito, 11 Feb 1989 (USNM). Paratypes: Costa Rica: Same location, 16 Mar 1989, 1 ♂ (BPS). Same location 17 Mar 1989, 1 ♂ (INBIO). Same location, 7 Apr 1989, 3 ♂,

2 ♀ (SWRC, BPS). Same location, 11 Apr 1990, 1 ♂ (INBIO). Same location, 27 Apr 1989, 1 ♂ (SWRC). Same location, 24 May 1989, 3 ♂ (BPS, SWRC). Same location, 28 May 1989, 1 ♀ (USNM). Same location, 22 Oct 1990, 1 ♂ (SWRC). Same location, 11 Nov 1989, 1 ♂ (INBIO). Same location, reared from eggs, 2 ♂, 2 ♀ (SWRC). Same location, 30 Aug 1990, J. Huisman, R. Blahnik, F. Quesada, 1 ♂ (UMSP). Guanacaste: Rio Los Ahogados, 470 m, 7 Mar 1986, R. Holzenthal, W. Fasth, 1 ♂ (UMSP). Hacienda la Pacifica, 75 m, 8 Jun 1973, G. Ekis, 1 ♂ (BYU). Monteverde, 22 Jun 1986, W. Hanson, 7 ♂ (USU).

**Diagnosis.**—The color pattern is similar to several species including *A. divisa* (Fig. 36) and *A. planicollis* (Fig. 91) but aedeagal features (Figs. 39, 85, 95) easily distinguish these species.

**Comments.**—Scientists at the Stroud Water Research Center reared two males and two females of this species from eggs collected at Estacion Maritza (J. Jackson, pers. comm.). The first egg mass collected 26 Aug 1992 produced a female on 18 Feb 1993 and a male on 11 Mar 1993. The second egg mass from 29 Nov 1992 produced a male on 14 May 1994 and a female on 3 Jun 1994. The nymphal description is based on exuviae from these specimens.

*Anacroneuria perplexa*, new species  
Figs. 86–90, 179–180

**Adult habitus.**—Dark head pattern covers ocelli and extends anterolaterally to lappets; small pale spot located in center of head. Pronotum mostly brown but with inconspicuous mesal yellow band (Fig. 86). Wing membrane brown, veins brown.

**Male.**—Forewing length 8 mm. Hammer absent or reduced to obscure membranous spot (Fig. 87). Aedeagal apex trilobed, lateral lobes small and ear shaped. Dorsal keel well developed, hooks enlarged and somewhat chelate (Figs. 88–90, 179–180).

**Female.**—Unknown.

**Nymph.**—Unknown.

**Etymology.**—The species name, meaning tangled or confused, refers to the initial difficulty experienced in separating this species from other small, dark forms with poorly developed hammers.

**Types.**—Holotype ♂ (USNM) and 2 ♂ paratypes (UMSP) from Costa Rica, Limon, Rio Barilla, ca. 8 km W B-line, 30 m, 31 Jan 1986, R. Holzenthal, J. Morse, W. Fasth. Additional paratypes: Costa Rica: Limon: Reserva Biol. Hitoy-Cerere, Rio Cerere, 90 m, 23 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 8 ♂ (UMSP, BPS). Rio Banano, 16 km WSW Bomba, 150 m, 26 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, (UMSP). Puntarenas: Rio Jaba, 1.4 km W Las Cruces, 1150 m, 14 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂ (INBIO). Villa Neilly, 21 Jun 1964, R. Woodruff, 1 ♂ (FSCA). San Jose: Escazu, 7–10 Apr 1988, F. D. Parker, 1 ♂ (USU).

**Diagnosis.**—A male paratype of *A. crenulata* from Temescaltepec, Mexico, is very similar to this species and distinct from the allotype of *A. crenulata*. The Mexican specimen differs from Costa Rican specimens most conspicuously in having long slender aedeagal hooks. Additional comments are given under *A. exquisita*.

*Anacroneuria planicollis* Klapálek  
Figs. 91–95, 147

*Anacroneuria planicollis* Klapálek, 1923:  
22. Lectotype ♂, Sierra du Naya, Mexico  
(NMP).

*Anacroneuria dampfi* Jewett, 1958:165.  
New synonymy.

*Anacroneuria chiapasa* Jewett, 1958:166.  
New synonymy.

**Adult habitus.**—Head pattern usually with brown ocellar spot, shading to diffuse brown forward of ocelli; lappets brown. Median pronotal stripe brown, bordered by yellow; lateral brown stripes interrupted by scattered pale areas on disc and along margins (Fig. 91). Wing membrane transparent, veins brown except C and Sc pale.

**Male.**—Forewing length 14–15 mm.

Hammer thimble shaped, height subequal to basal diameter (Fig. 92). Aedeagal apex trilobed, mesal lobe slightly larger. Hooks slender, dorsal keel well developed (Figs. 93–95).

*Female*.—Forewing length 16–17 mm. Subgenital plate bilobed, lobes truncate to emarginate. Mesal sclerite of sternum nine T-shaped; lateral arms with long setae, stalk with fine short setae (Fig. 147).

*Nymph*.—Unknown.

*Material*.—Costa Rica; Monteverde, 22 Jun 1986, W. J. Hanson, 2 ♂ (USU). Alajuela: 20 km S Upala, 12 Feb–5 Mar 1991, F. Parker, 2 ♂ (USU). Puntarenas: Rio Bellavista, ca. 1.5 km NW Las Alturas, 1400 m, 15 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂ (UMSP). Same location, 8 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂, 2 ♀ (INBIO). Mexico: Sierra du Naya, L. Diguet, 1898, lectotype ♂, paralectotype ♀ (NMP). Nicaragua: Nuevosegovia, Dipilto, Dec 1986, J. Maes, 1 ♂ (USNM). Panama: Chiriquí, Cerro Punta, 3 mi N on Pan American Highway, 4 Apr 1954, G. Field, 1 ♂ (USNM).

*Comments*.—The type series included four male and three female specimens from Mexico and a female from Costa Rica (Klapálek 1923). Of these, a syntype male and female were found in the Natural History Museum, Prague and studied while on loan to P. Zwick. the male is designated as lectotype. Synonymy of the two Jewett (1958) species is based on study of the holotypes and male allotypes.

*Anacroneuria plutonis* (Banks)

Figs. 96–100, 148, 157, 181–182

*Neoperla plutonis* Banks, 1914:610. Lectotype ♀, La Trinidad, Costa Rica (MCZ).

*Forquilla tristani* Navas, 1932:29. New synonymy.

*Adult habitus*.—Head pattern dark brown from ocellar area to M-line except for pale oval spots lateral to ocelli; lappets connected by a diffuse brown band along anterior

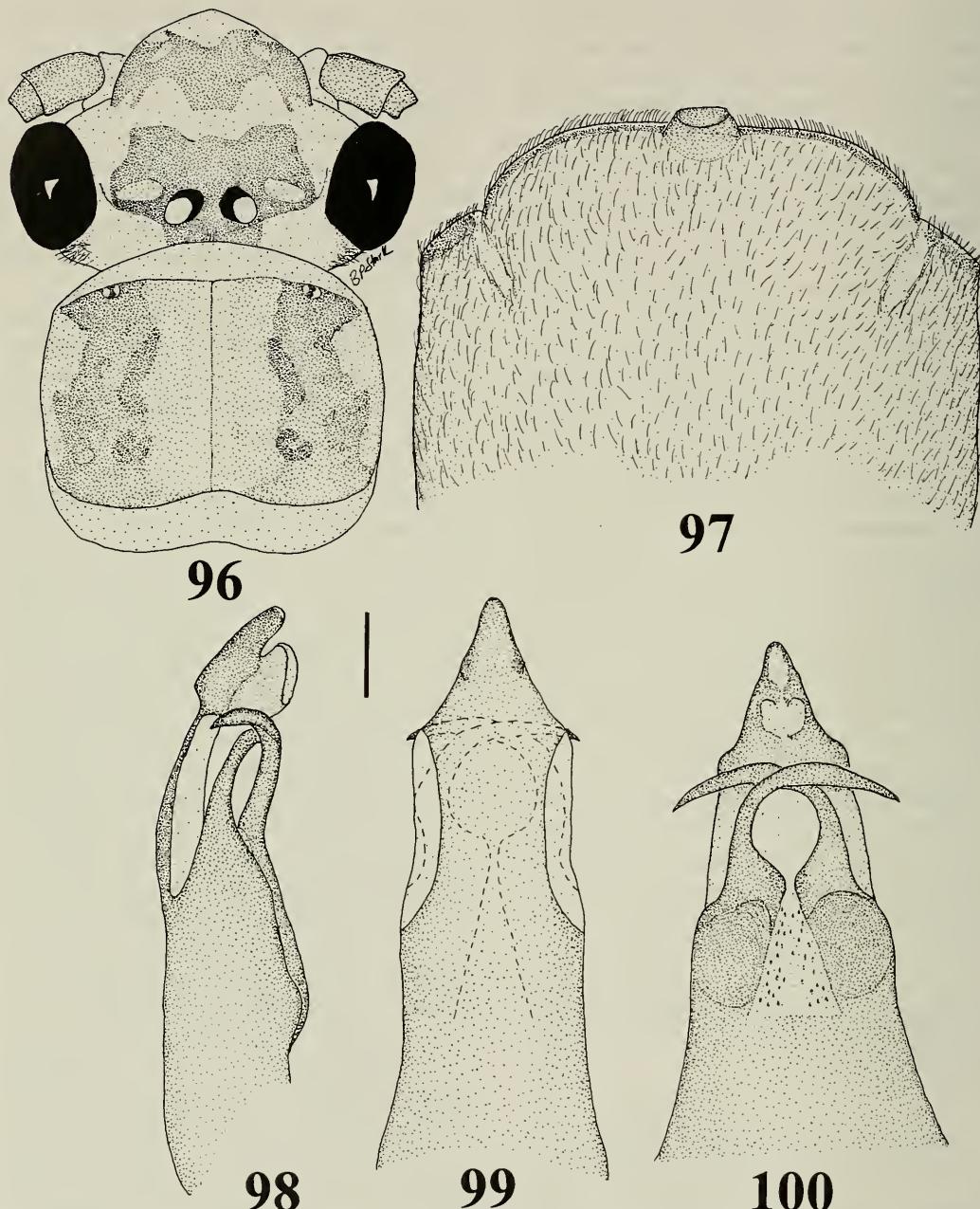
margins of M-line. Pronotum diffuse brown to dark brown but without distinct bands (Fig. 96). Wing membrane brown, veins brown.

*Male*.—Forewing length 19–21 mm. Hammer thimble shaped, height less than basal diameter (Fig. 97). Aedeagal apex simple, gradually tapered to a narrow tip. Hooks slender, dorsal keel absent (Figs. 98–100, 157, 181–182).

*Female*.—Forewing length 25–28 mm. Subgenital plate bilobed; lobes truncate, notch shallow and U-shaped. Transverse sclerite absent, mesal sclerite T-shaped, sparsely setose (Fig. 148).

*Nymph*.—Unknown.

*Material*.—Costa Rica: Alajuela: Rio Sarapiqui, ca. 2 km SE Cariblanco, 710 m, 22 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂, 1 ♀ (BPS). Quebrada Latas, 8.9 km NE Bajos del Toro, 1030 m, 6 Sep 1990, R. Holzenthal, R. Blahnik, J. Huisman, 2 ♂ (UMSP). Reserva Forestal San Ramon, Rio San Lorencito, 6–10 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 4 ♂ (UMSP, INBIO). Cartago: Reserva Tapanti, Quebrada Palmitos, 1400 m, 24 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 1 ♀ (UMSP). Same location, 2 Jun 1990, R. Holzenthal, R. Blahnik, F. Munoz, 7 ♂ (BPS, INBIO). Guanacaste: Estacion Maritza, Rio Tempisque, 14 May 1989, 1 ♂ (SWRC). Parque Nacional Guanacaste, Maritza, Rio Tempisque, 550 m, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen, 1 ♂ (UMSP). Puntarenas: Rio Bellavista, ca. 1.5 km NW Las Alturas, 1400 m, 8 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (UMSP). Rio Coton, Las Alturas, 1360 m, 16 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 1 ♂ (UMSP). Same location, 18 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman, 1 ♂ (BPS). San Jose: El Salvaje, Rio Tabarcia, 8 km E Palmichal, 1650 m, 19 Jan 1992, R. Holzenthal, K. Kjer, F. Quesada, 11 ♂, 3 ♀ (BPS, UMSP, INBIO). Rio Parrita Chiquita, 1990 m, 18 Jun 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂, 1 ♀ (USNM).



Figs. 96–100. *A. plutonis* structures. 96. Head and pronotum. 97. Male sternum 9. 98. Aedeagus, lateral. 99. Aedeagus, dorsal. 100. Aedeagus, ventral. Scales: 0.6 mm (96), 0.3 mm (97), 0.15 mm (98–100).

*Comments.*—*Anacroneuria plutonis* and *A. tristani* are both large dark species described from Costa Rican specimens. Navas (1932) reports the forewing length of *A. tristani* females is 18.5 mm but the type specimen is

actually larger than the *A. plutonis* lectotype from La Trinidad (L. Benedetto, pers. comm.). I have not seen the specimens identified by Jewett (1958) as *A. tristani* but the four lobed female subgenital plate mentioned

in Jewett's description clearly indicates this material was misidentified.

*Anacroneuria talamanca*, new species  
Figs. 101–105, 149

**Adult habitus.**—Ocellar area covered by a small brown quadrangle; lateral margins of frons diffuse brown, lappets brown. Median pronotal stripe yellow, lateral stripes brown (Fig. 101). Wing membrane transparent veins brown.

**Male.**—Forewing length 7–8 mm. Hammer thimble shaped, height subequal to basal diameter (Fig. 102). Aedeagal apex simple, slender with small dorsal keel. Hooks enlarged and ventrally keeled (Figs. 103–105).

**Female.**—Forewing length 9–10 mm. Subgenital plate bilobed; lobes truncate, median notch shallow and V-shaped. Transverse sclerite of sternum nine poorly developed, mesal sclerite with long stem, lateral arms poorly developed and sparsely setose (Fig. 149).

**Nymph.**—Unknown.

**Etymology.**—The species name, based on the Cordillera Talamanca, is used as a noun in apposition.

**Types.**—Holotype ♂ from Costa Rica, San Jose, Reserva Biol. Carara, Rio Carara, Carara, 200 m, 14 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman (USNM). Paratypes: Costa Rica: Heredia: Estacion Biol. La Selva, Rio Puerto Viejo, 30 m, 10 Feb 1986, R. Holzenthal, 1 ♂ (UMSP). La Selva, 14 Jun 1986, W. J. Hanson, 1 ♂ (USU). Panama: Bocas del Toro: Miramar, 1 May 1979, H. Wolda, 1 ♂, 2 ♀ (BYU). Same location, 22 May 1979, H. Wolda, 1 ♀ (BYU).

**Diagnosis.**—The aedeagus of this species is similar to that of the allotype of *A. crenulata* Jewett and to the holotype of *A. litura* (Pictet) (Zwick 1972). *A. talamanca* differs from these in having the apical aedeagal section beyond the hooks about as long as wide; in *A. crenulata* and *A. litura* this section is distinctly longer than wide and has

a dorsal keel more than twice the length of the keel of *A. talamanca*. In addition, the female holotype of *A. crenulata* has a four lobed subgenital plate whereas the subgenital plate of *A. talamanca* is bilobed.

*Anacroneuria tornada*, new species  
Figs. 106–110

**Adult habitus.**—Diffuse brown area forward of ocelli, lappets brown. Narrow brown median pronotal stripe bordered by narrow yellow stripes; midlateral stripes brown, margins pale (Fig. 106). Wing membrane transparent, veins brown.

**Male.**—Forewing length 16 mm. Hammer a low disc (Fig. 107). Aedeagal apex multilobed, curved abruptly ventrad between hook tips. Apex in dorsal aspect somewhat truncate, keel absent. Hooks stout, enlarged apically (Figs. 109–110).

**Female.**—Unknown.

**Nymph.**—Unknown.

**Etymology.**—Tornado, Spanish for renegade, refers to the unusual aedeagal apex of this species and is used as a noun in apposition.

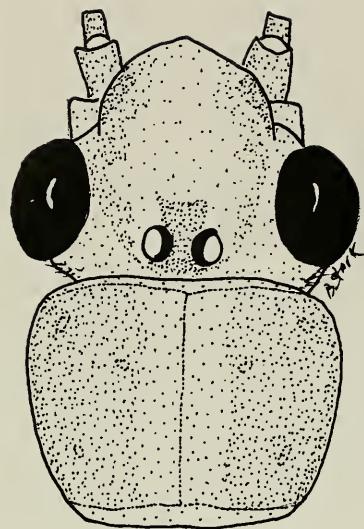
**Types.**—Holotype ♂ from Costa Rica, Cartago, Reserva Tapanti, Quebrada Palmitos, 1400 m, 2 Jun 1990, R. Holzenthal, R. Blahnik, F. Munoz (USNM).

**Diagnosis.**—The color pattern of *A. tornado* is similar to that of *A. maritza* (Fig. 81), *A. divisa* (Fig. 36) and *A. planicollis* (Fig. 51) but the aedeagal apex clearly distinguishes these species (Figs. 39, 85, 95, 110).

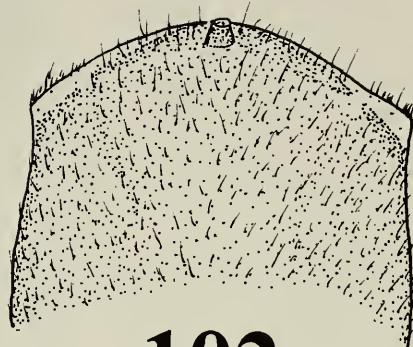
*Anacroneuria uatsi*, new species  
Figs. 111–115, 150, 153–154

**Adult habitus.**—Head yellow except dark areas on lappets and over ocelli. Median third of pronotum pale, lateral margins brown (Fig. 111). Wing membrane transparent, veins brown except pale C and Sc.

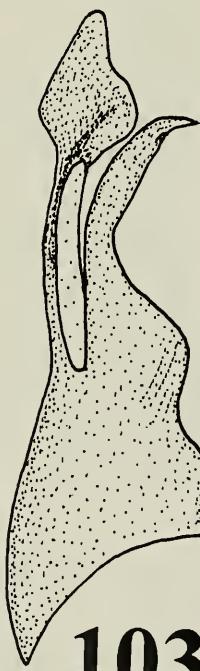
**Male.**—Forewing length 9 mm. Hammer thimble shaped, length greater than basal diameter (Fig. 112). Aedeagal apex a slender, finger shaped structure arising from a



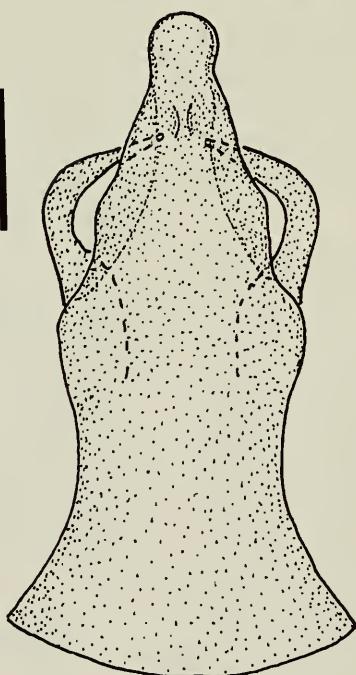
101



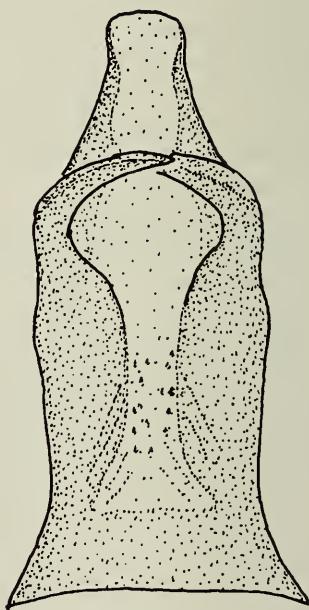
102



103

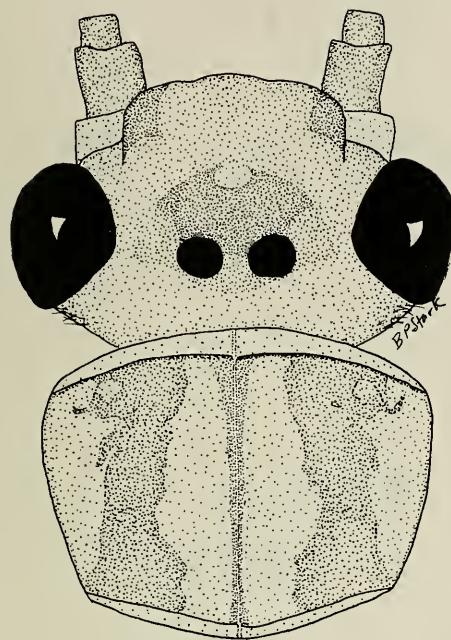
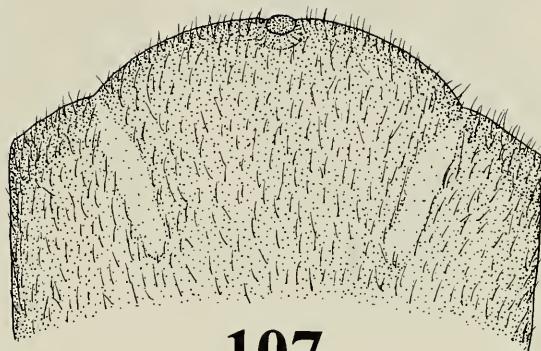
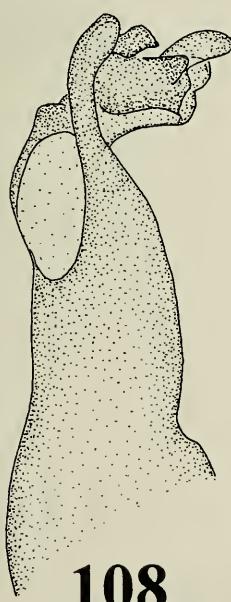
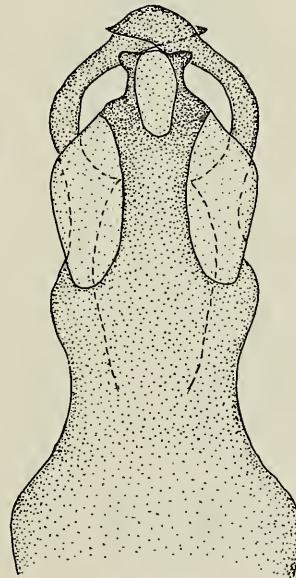
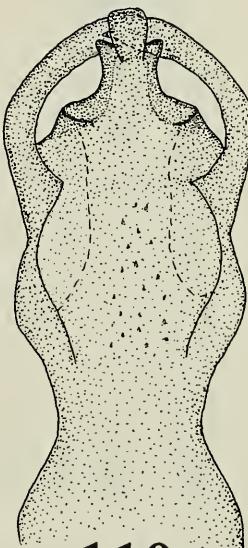


104

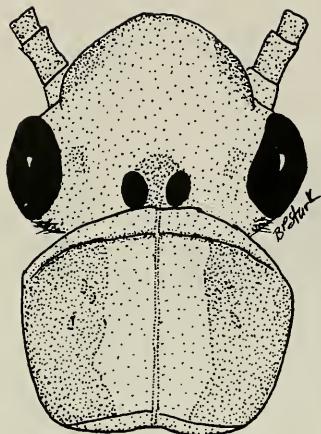


105

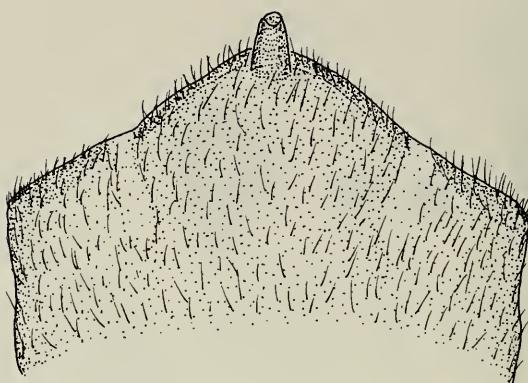
Figs. 101-105. *A. talamanca* structures. 101. Head and pronotum. 102. Male sternum 9. 103. Aedeagus, lateral. 104. Aedeagus, dorsal. 105. Aedeagus, ventral. Scales: 0.6 mm (101), 0.3 mm (102), 0.15 mm (103-105).

**106****107****108****109****110**

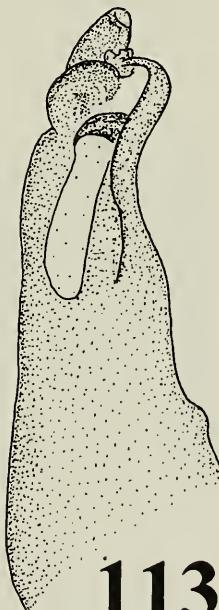
Figs. 106–110. *A. tornada* structures. 106. Head and pronotum. 107. Male sternum 9. 108. Aedeagus, lateral. 109. Aedeagus, dorsal. 110. Aedeagus, ventral. Scales: 0.6 mm (106), 0.3 mm (107), 0.15 mm (108–110).



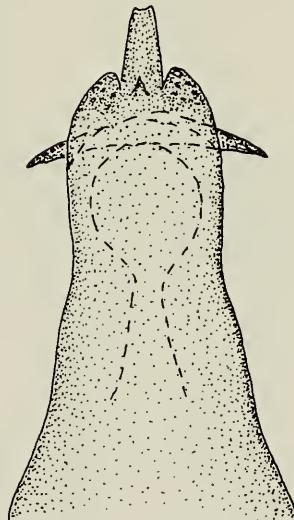
111



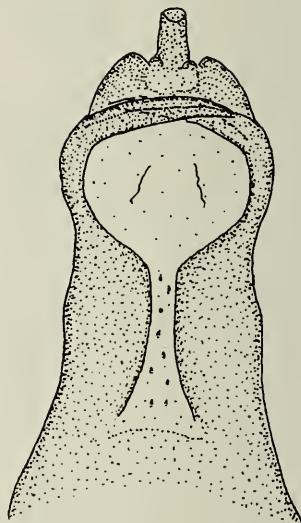
112



113



114



115

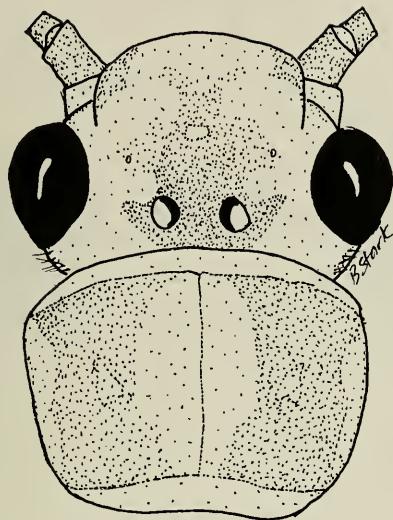
Figs. 111–115. *A. uatsi* structures. 111. Head and pronotum. 112. Male sternum 9. 113. Aedeagus, lateral. 114. Aedeagus, dorsal. 115. Aedeagus, ventral. Scales: 0.6 mm (111), 0.3 mm (112), 0.15 mm (113–115).

broad base with rounded, slightly projecting shoulders. Dorsomesal keel minute, triangular, hooks slender (Figs. 113–115).

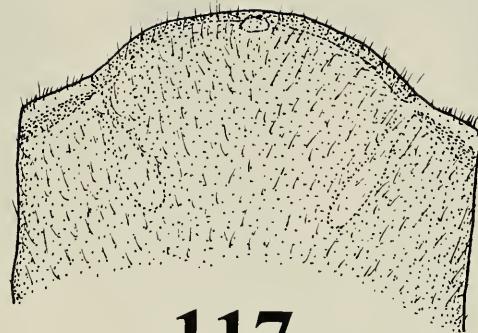
*Female*.—Forewing length 10 mm. Subgenital plate with four subequal lobes.

Transverse sclerite of sternum nine narrow; mesal T-shaped sclerite setose (Fig. 150).

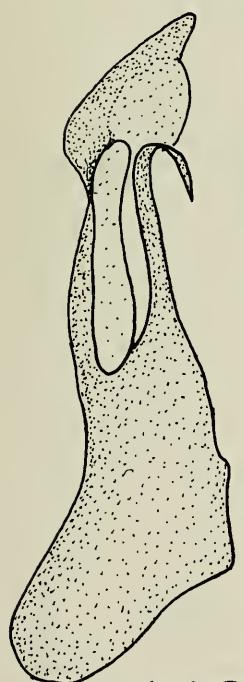
*Nymph*.—Body length 9–11 mm. Head forward of ocelli dark brown except for incomplete M-line and anterior margin. Pro-



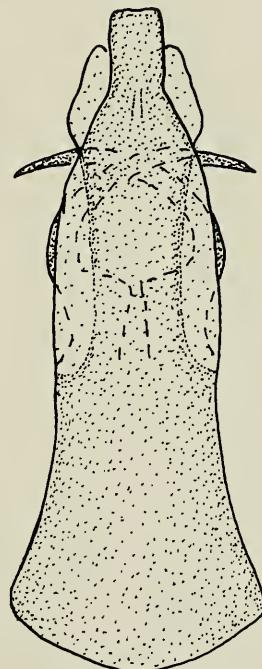
116



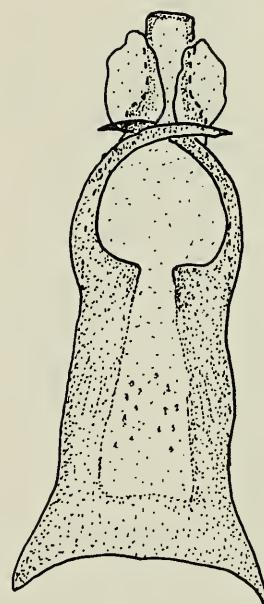
117



118

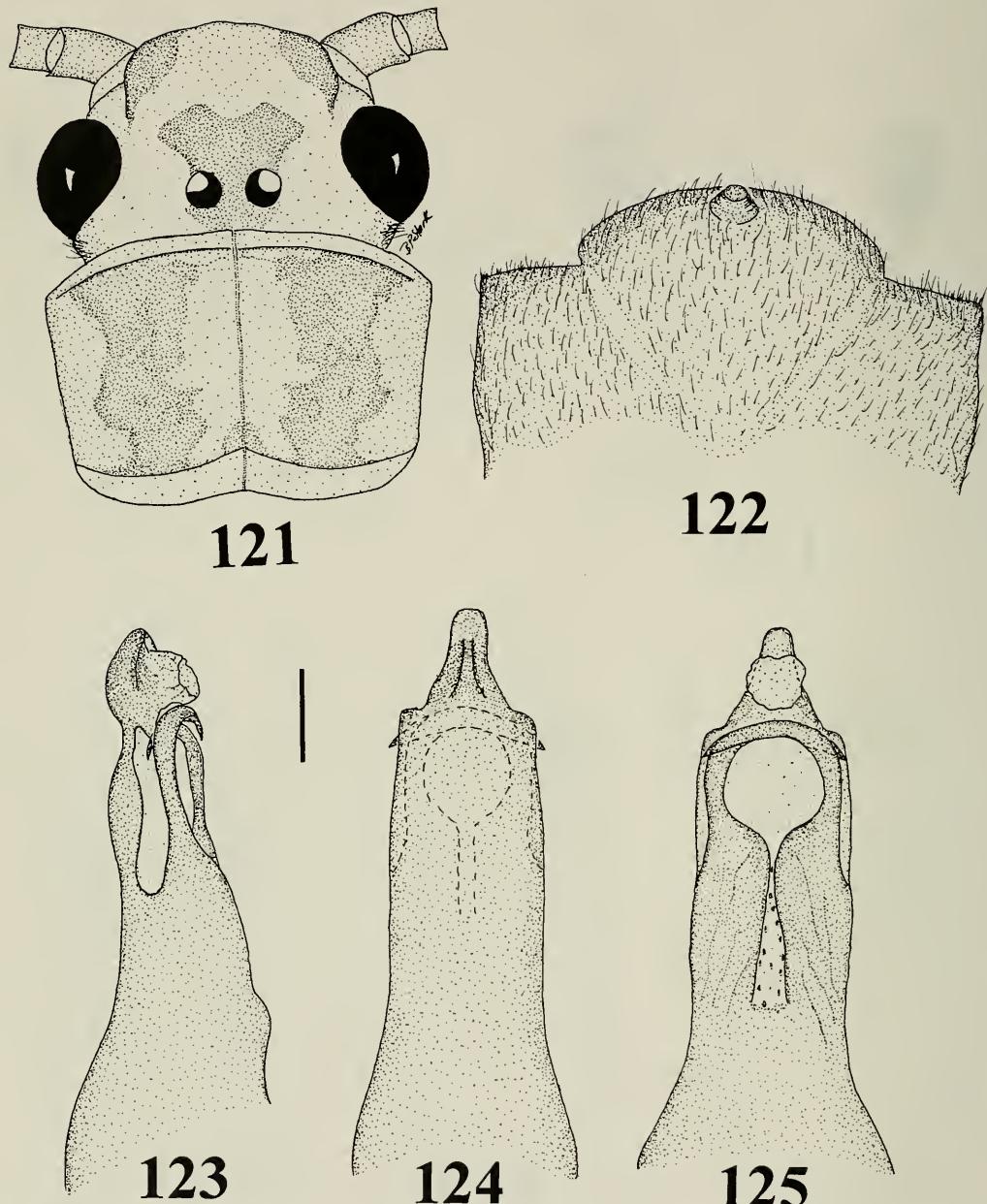


119



120

Figs. 116-120. *A. varilla* structures. 116. Head and pronotum. 117. Male sternum 9. 118. Aedeagus, lateral. 119. Aedeagus, dorsal. 120. Aedeagus, ventral. Scales: 0.6 mm (116), 0.3 mm (117), 0.15 mm (118-120).



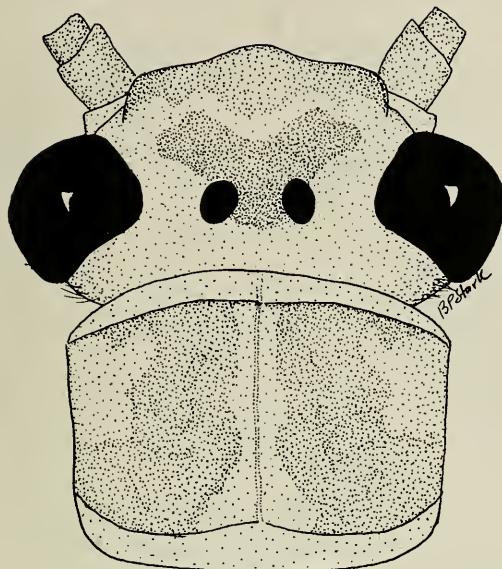
Figs. 121-125. *A. ventana* structures. 121. Head and pronotum. 122. Male sternum 9. 123. Aedeagus, lateral. 124. Aedeagus, dorsal. 125. Aedeagus, ventral. Scales: 0.6 mm (121), 0.3 mm (122), 0.15 mm (123-125).

notum predominantly brown (Fig. 153). Anterodorsal femoral bristles grouped in irregular basal and apical patches and a median transverse row (Fig. 154).

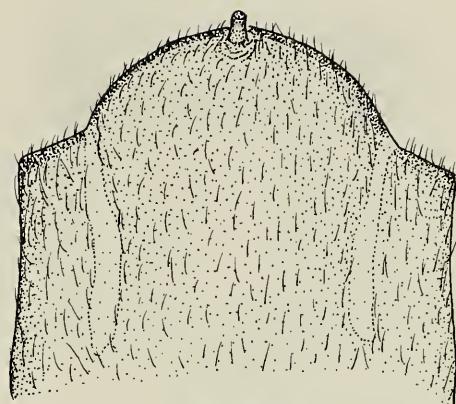
**Etymology.**—The species name, based on

the type locality, is used as a noun in apposition.

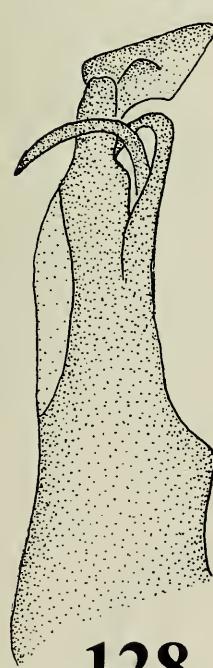
**Types.**—Holotype ♂ and ♂ paratype from Costa Rica, Limon, Rio Uatsi, 8 km W Bribri, 60 m, 25 Mar 1987, R. Holzen-



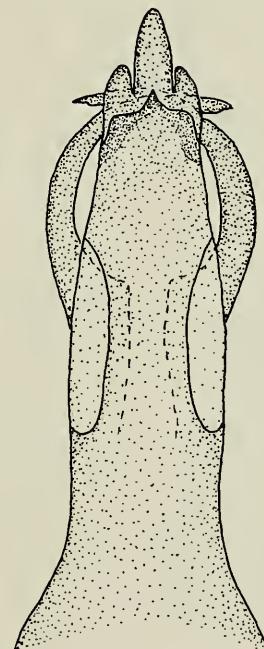
126



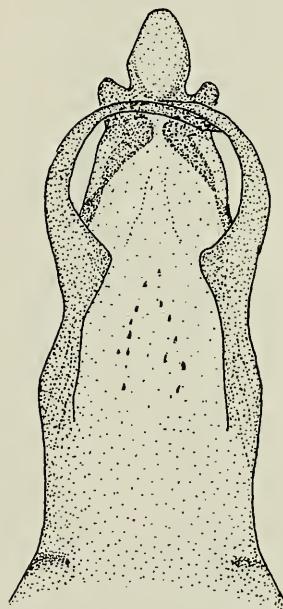
127



128

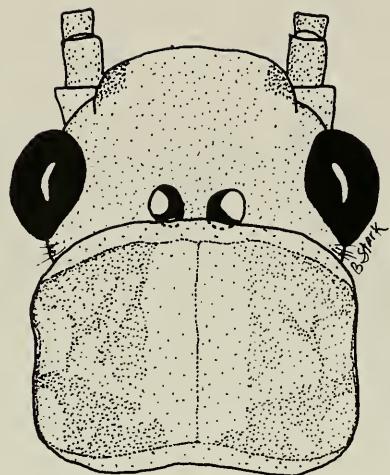


129

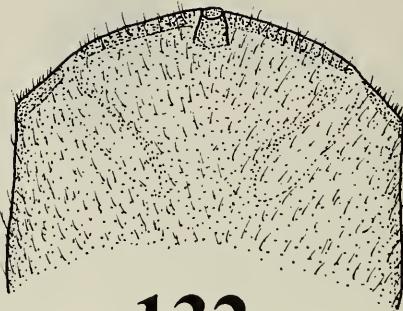


130

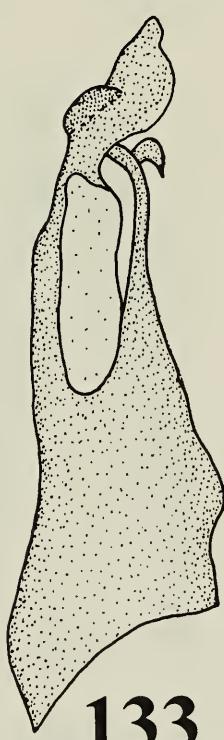
Figs. 126-130. *A. zapata* structures. 126. Head and pronotum. 127. Male sternum 9. 128. Aedeagus, lateral. 129. Aedeagus, dorsal. 130. Aedeagus, ventral. Scales: 0.6 mm (126), 0.3 mm (127), 0.15 mm (128-130).



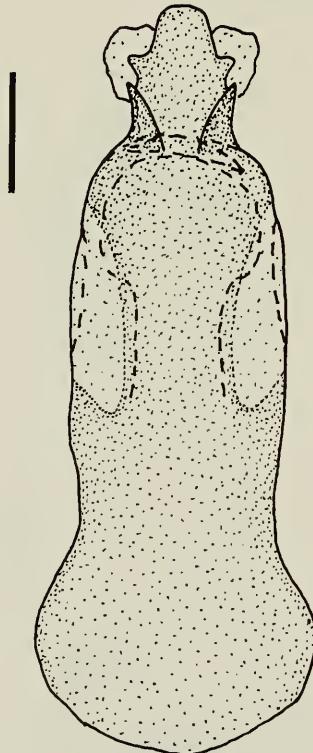
131



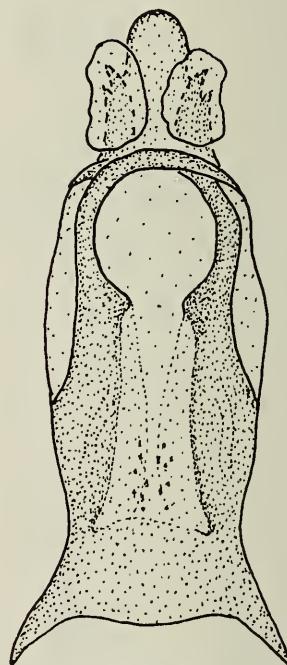
132



133

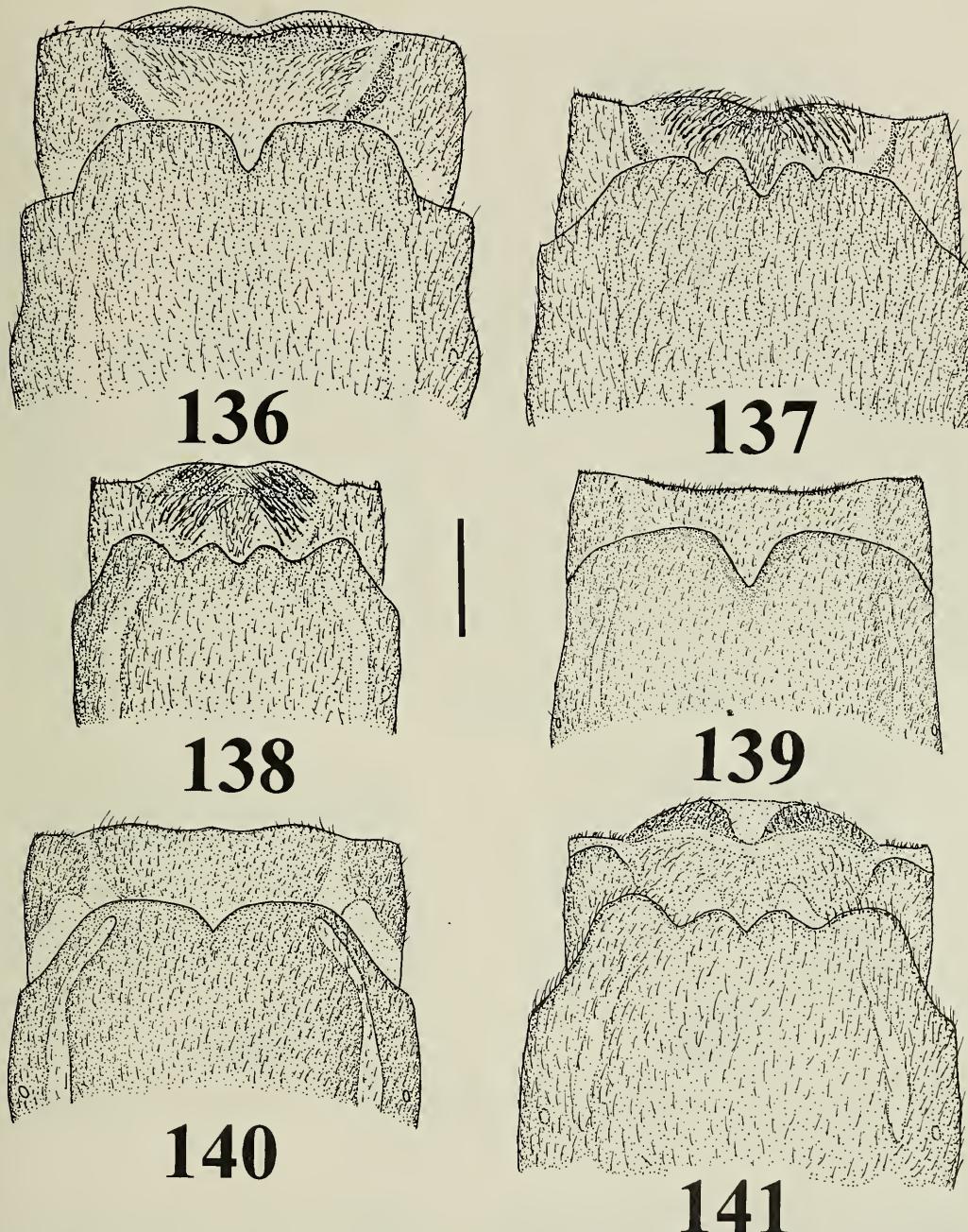


134



135

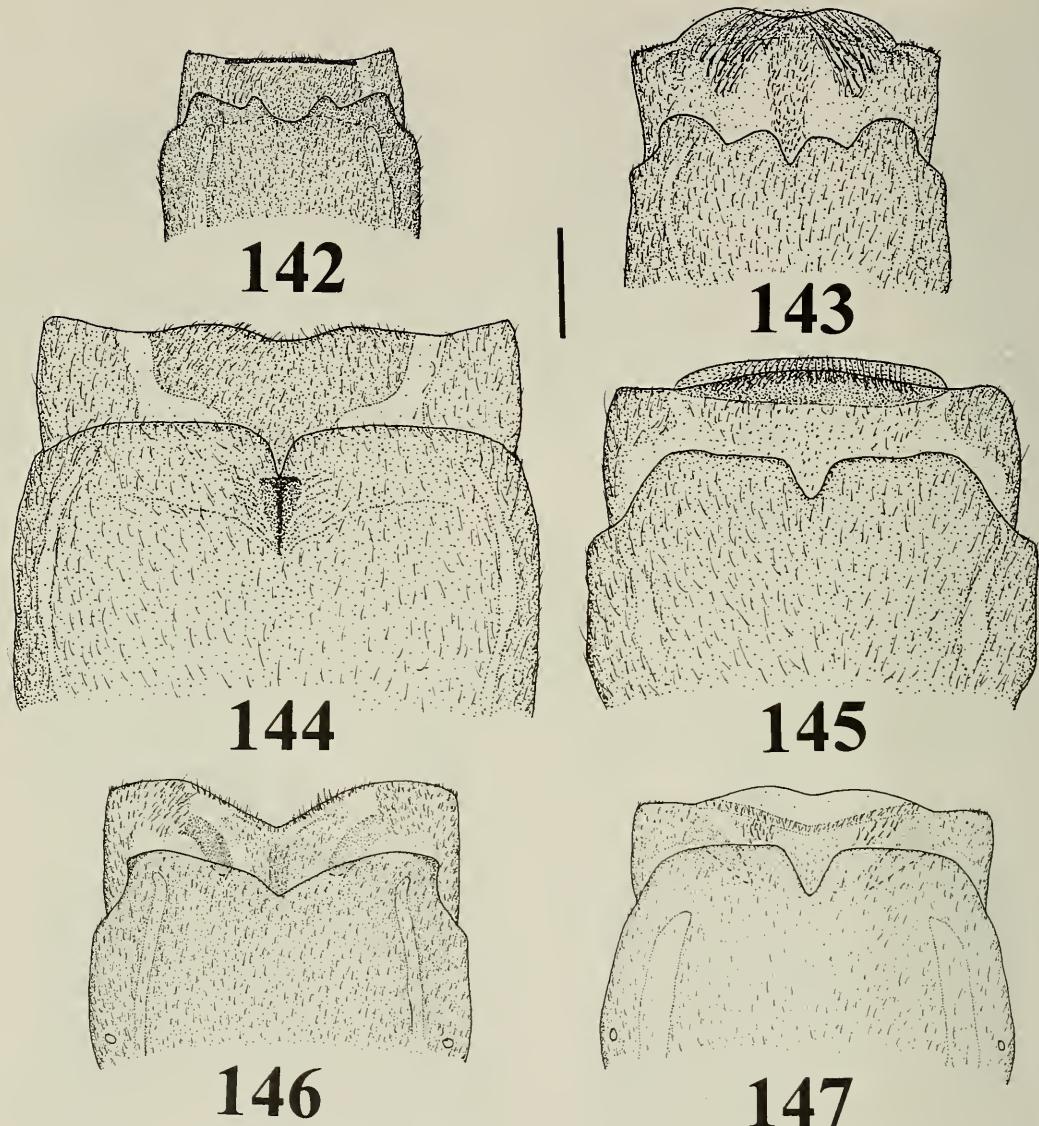
Figs. 131-135. *A. zarpa* structures. 131. Head and pronotum. 132. Male sternum 9. 133. Aedeagus, lateral. 134. Aedeagus, dorsal. 135. Aedeagus, ventral. Scales: 0.6 mm (131), 0.3 mm (132), 0.15 mm (133-135).



Figs. 136–141. *Anacroneuria* female sterna 8 and 9. 136. *A. acutipennis*. 137. *A. annulipalpis*. 138. *A. benedettoi*. 139. *A. blanda*. 140. *A. varilla*. 141. *A. divisa*. Scale = 0.6 mm.

thal, S. Hamilton, M. Heyn (USNM). Additional paratypes: Costa Rica: Guanacaste: Rio Tempisque, 3 km S route 1, 75 m, 6 Mar 1986, R. Holzenthal, W. Fasth, 2 ♂

(UMSP). Las Canas, Rio Carabici, 26 Jul 1967, O. S. Flint, 1 ♂ (USNM). Limon: E.A.R.T.H., Rio Destierra, Pozo Azul, 15 m, 5 Feb 1992, R. Holzenthal, F. Munoz,

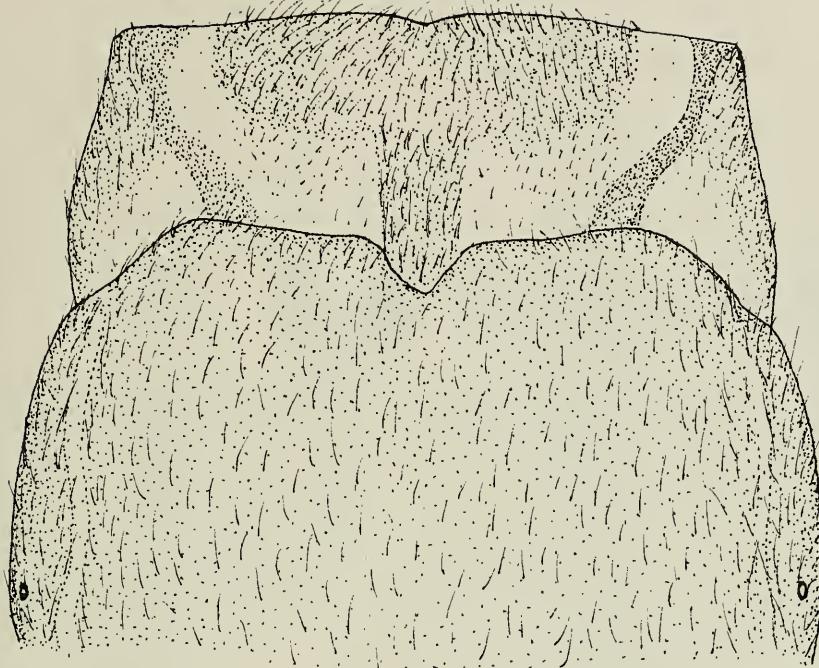


Figs. 142-147. *Anacroneuria* female sterna 8 and 9. 142. *A. harperi*. 143. *A. holzenthali*. 144. *A. magnirufa*. 145. *A. marca*. 146. *A. maritza*. 147. *A. planicollis*. Scale = 0.6 mm.

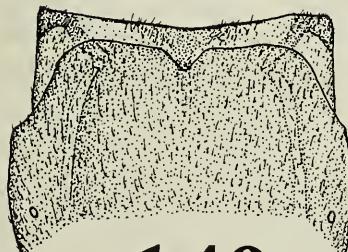
K. Kjer, 1 ♂, 1 ♂ (BPS). Reserva Biol. Hito-Cerere, Rio Cerere, 90 m, 23 Mar 1987, R. Holzenthal, S. Hamilton, M. Heyn, 1 ♂ (UMSP). Rio Uatsi, W Uatsi, 50 m, 2 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 2 nymphs (UMSP). Puntarenas: 2.8 mi E Golfito, 18 Jul 1967, O. S. Flint, 1 ♂ (USNM). Rio Rincon, 6.5 km S Rincon, 20 m, 7 Apr 1987, R. Holzenthal, S. Hamilton,

M. Heyn, 1 ♂ (INBIO). Quebrada Pita, 3 km W Golfito, 15 m, 15 Feb 1986, R. Holzenthal, J. Morse, W. Fasth, 22 ♀ (UMSP, INBIO). Quebrada Portera, N Grande Portera, 5 Jul 1992, T. Shepard, 1 ♂ (CSU).

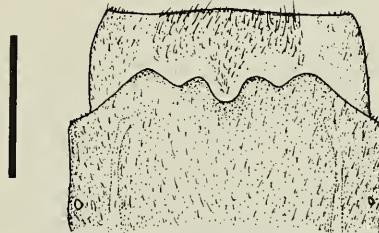
*Diagnosis*.—See under *A. curiosa*. The nymphs were associated by dissection of male genitalia from a pre-emergent individual.



148



149



150

Figs. 148–150. *Anacroneuria* female sterna 8 and 9. 148. *A. plutoensis*. 149. *A. talamanca*. 150. *A. uatsi*. Scale = 0.6 mm.

*Anacroneuria varilla*, new species

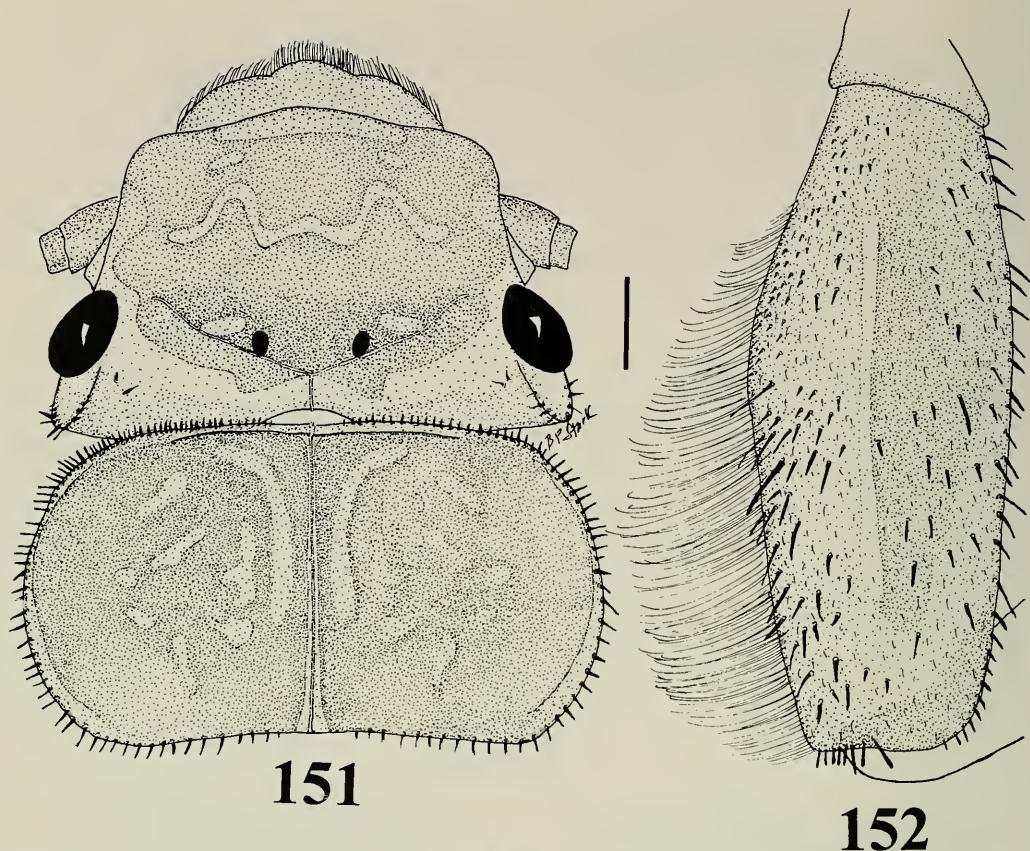
Figs. 116–120, 140, 183–184

**Adult habitus.**—Head yellow except for lappets and diffuse quadrangular brown spot over ocelli. Pronotum with irregular midlateral dark bands and a pale mesal band (Fig. 116). Wing membrane transparent, veins brown.

**Male.**—Forewing length 9–10 mm.

Hammer reduced to a low membranous mound or short thimble (Fig. 117). Aedeagal apex a simple slender scoop with a pair of large ventral membranous processes; inconspicuous lateral notches occur at base of tip. Hooks very slender, dorsal keel inconspicuous (Figs. 118–120, 183–184).

**Female (putative).**—Forewing length 13 mm. Subgenital plate bilobed, notch shal-



Figs. 151–152. *A. maritza* nymphal structures. 151. Head and pronotum. 152. Fore femur. Scales: 0.6 mm (151), 0.3 mm (152).

low. Transverse sclerite of sternum nine indistinct, mesal sclerite with sparse scattered setae (Fig. 140).

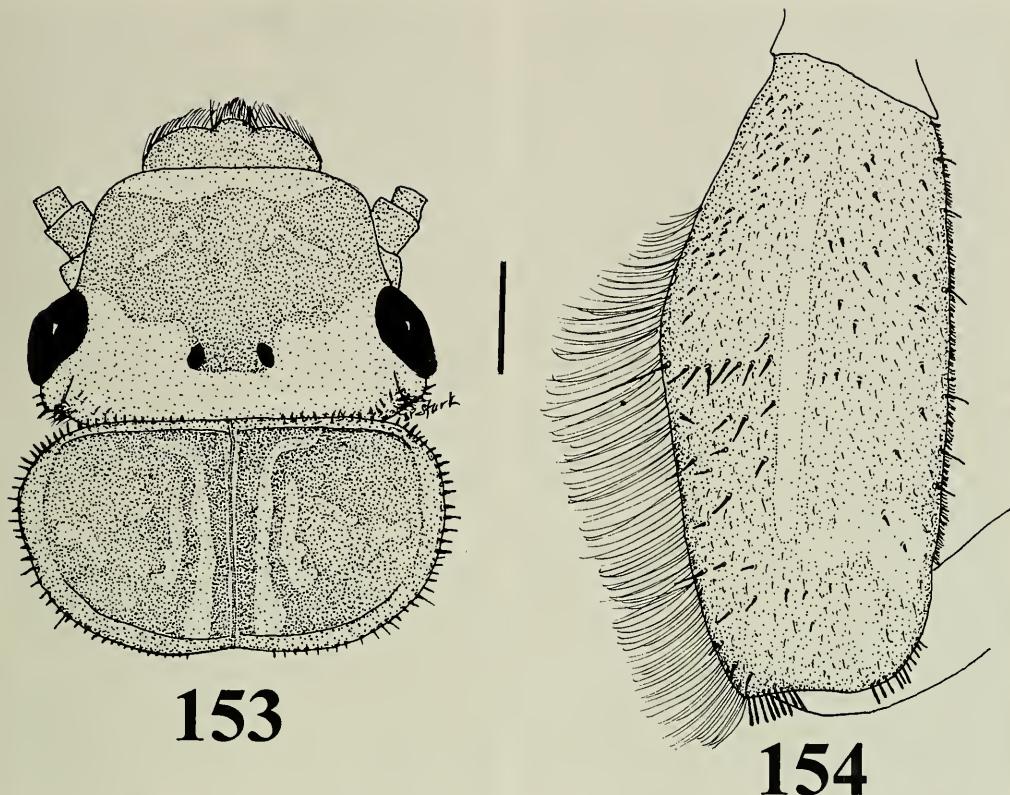
*Nymph*.—Unknown.

*Etymology*.—The species name, Spanish for small rod, refers to the thin aedeagal hooks and is used as a noun in apposition.

*Types*.—Holotype ♂ (USNM) and 6 ♂ paratypes (UMSP) from Costa Rica, Guanacaste, Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550 m, 19 Jul 1987, R. Holzenthal, J. Morse, P. Clausen. Additional paratypes: Costa Rica: Guanacaste: Parque Nacional Guanacaste, Rio Orosi, 700 m, 22 May 1990, R. Holzenthal, R. Blahnik, 1 ♂ (BPS). Parque Nacional Guanacaste, Maritza, Rio Tempisquito, 550

m, 17 Jun 1988, C. M. Flint, O. S. Flint, R. Holzenthal, 3 ♂ (USNM). Estacion Maritza, Rio Tempisquito, 8 Feb 1989, 2 ♂ (SWRC). Same location, 17 Mar 1989, 3 ♀ (INBIO). Same location, 27 Apr 1989, 3 ♂, 2 ♀ (BPS, INBIO, SWRC). Same location, 22 Oct 1990, 1 ♂ (SWRC). Same location, 11 May 1990, 12 ♂ (SWRC, INBIO). Panama: Chiriquí Province: Cuenca Fortuna, Quebrada Arena 3500', 23 May 1985, R. W. Flowers, 1 ♂ (BPS).

*Diagnosis*.—The hammer shape and general coloration of this species are similar to *A. perplexa*, however the aedeagal hooks of that species are stout (Fig. 90) and the apex is trilobed (Figs. 89–90). These features easily distinguish *A. varilla* which has slender hooks and a simple apex (Figs. 119–120).



Figs. 153–154. *A. uatsi* nymphal structures. 153. Head and pronotum. 154. Fore femur. Scales: 0.6 mm (153), 0.3 mm (154).

*Anacroneuria ventana*, new species

Figs. 121–125

**Adult habitus.**—Dark Y-shaped spot covers ocelli and extends to M-line; lappets dark brown. Broad median pronotal band pale, irregular midlateral bands brown, marginal areas pale (Fig. 121). Wing membrane brown except for transparent window beyond cord, veins brown.

**Male.**—Forewing length 15 mm. Hammer thimble shaped, height less than basal diameter (Fig. 122). Aedeagal apex simple, tapered to a small rounded tip with a membranous ventral process. Hooks slender, dorsal keel moderately developed (Figs. 123–125).

**Female.**—Unknown.

**Nymph.**—Unknown.

**Etymology.**—The species name, Spanish for window, refers to the transparent apical

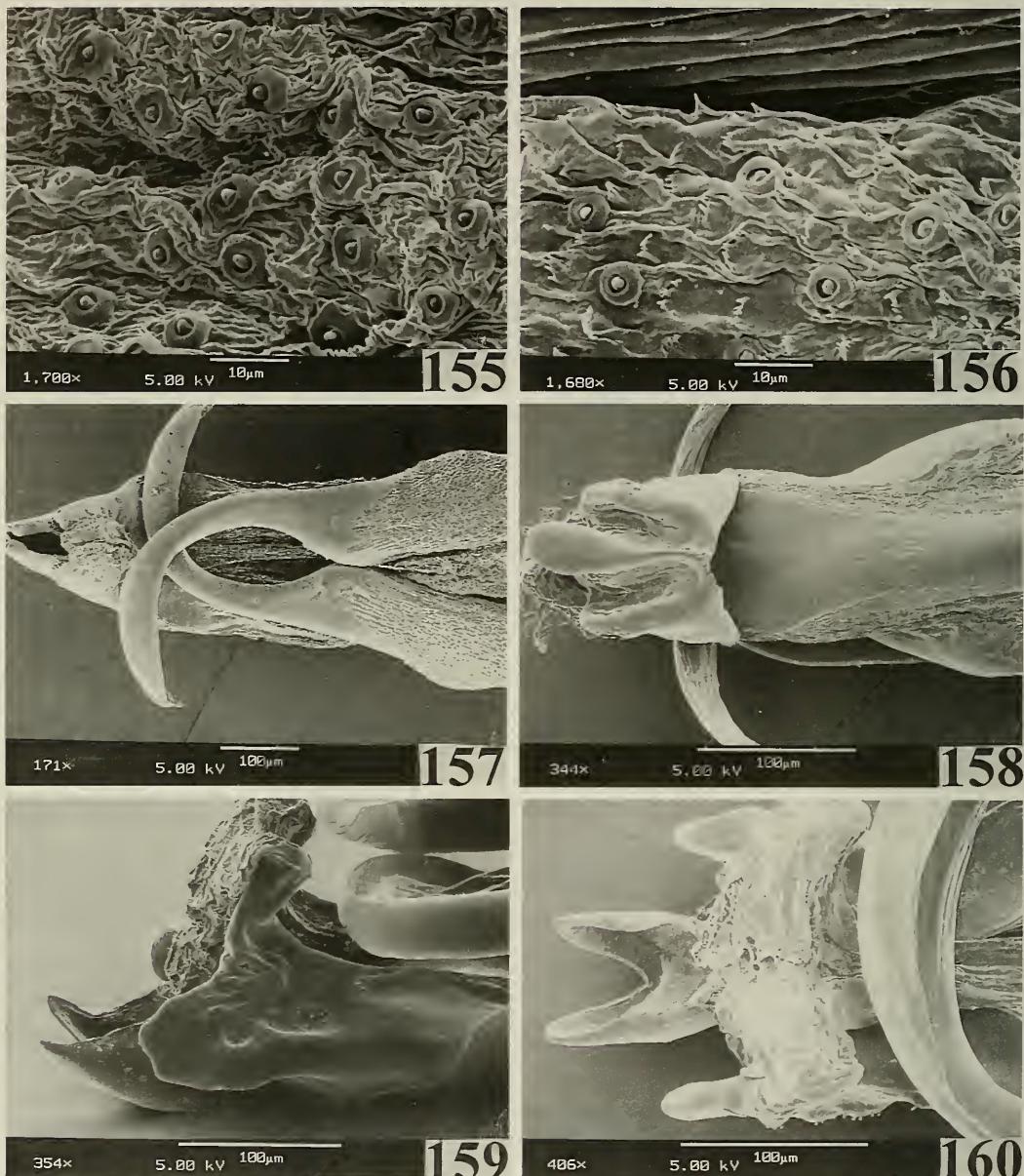
area in the wing membrane and is used as a noun in apposition.

**Types.**—Holotype ♂ from Costa Rica, Alaqua, Rio Peje, ca. 1 km SE San Vicente, 1450 m, 14 Feb 1992, R. Holzenthal, F. Munoz, K. Kjer (USNM). Paratype: Costa Rica: Cartago: Reserva Tapanti, Quebrada Palmitos, 1400 m, 24 Mar 1991, R. Holzenthal, F. Munoz, J. Huisman 1 ♂ (UMSP). San Jose: Parque Nacional Carrillo, Rio Zurqui, 1650 m, 5 Feb 1986, J. Morse, W. Fasth, 1 ♂ (BPS).

**Diagnosis.**—See under *A. marca*.

*Anacroneuria zapata*, new species  
Figs. 126–130

**Adult habitus.**—Diffuse V-shaped pattern extends from ocelli forward to M-line; lappets and anterior margin of head pale brown. Pronotum brown except for narrow



Figs. 155–160. *Anacroneuria* aedeagal structures. 155. *A. magnirufa* sensilla patch between hooks. 156. *A. benedetto* sensilla and microtrichia patch between hooks. The ridges above the patch are on the adjacent ventral sclerite. 157. *A. plutonis* ventral. 158. *A. curiosa* dorsal. 159. *A. acutipennis* apex, lateral. 160. *A. acutipennis* apex, ventral.

mesal stripe and anterolateral margins (Fig. 126). Wing membrane transparent, veins brown except for pale C and Sc.

**Male.**—Forewing length 13–14 mm. Hammer cylindrical (Fig. 127). Ventral aedeagal apex trilobed, hooks slender. Small

dorsal keel projects apically along mesal lobe; lateral lobes of apex ear shaped (Figs. 128–130).

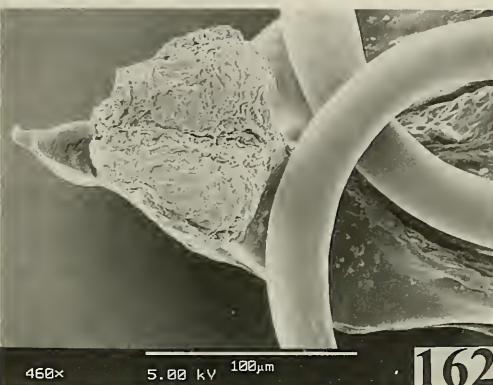
**Female.**—Unknown.

**Nymph.**—Unknown.

**Etymology.**—Zapata, Spanish for shoe,



450x 5.00 kV 100µm



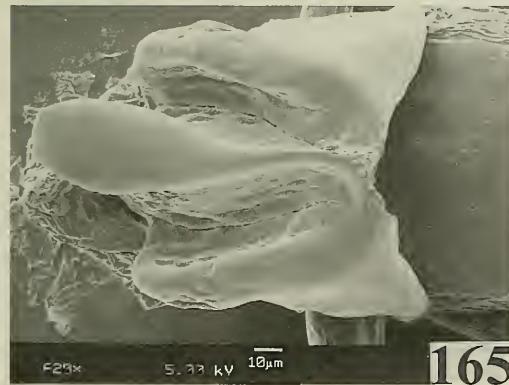
460x 5.00 kV 100µm



280x 5.00 kV 100µm



220x 5.00 kV 100µm



520x 5.00 kV 10µm



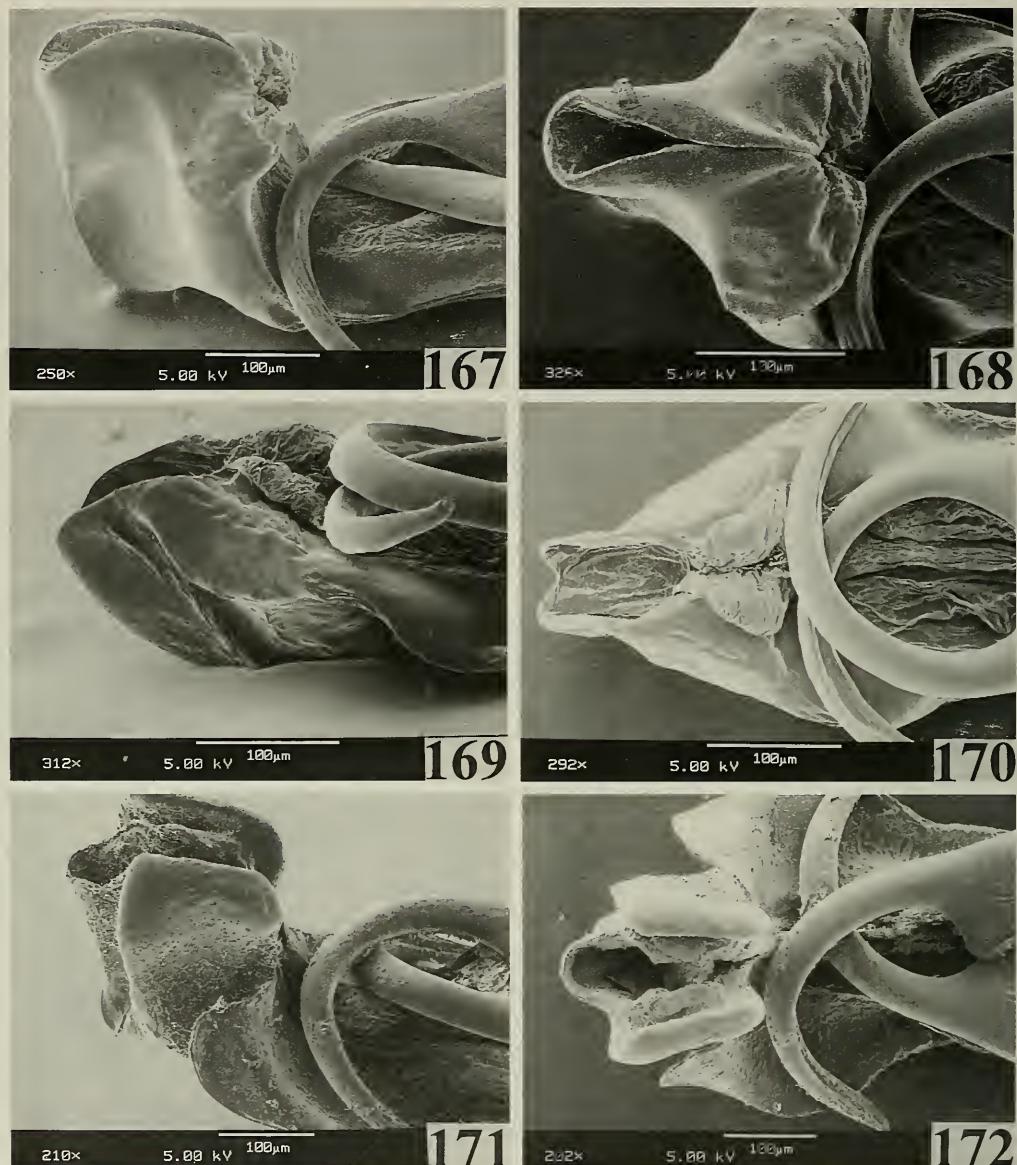
650x 5.00 kV 10µm

Figs. 161–166. *Anacroneuria* aedeagal structures. 161. *A. annulipalpis* apex, lateral. 162. *A. annulipalpis* apex, ventral. 163. *A. benedettoi* apex, lateral. 164. *A. benedettoi* apex, dorsal. 165. *A. curiosa* apex, dorsal. 166. *A. curiosa* apex, ventral.

refers to the slipper shaped lateral aspect of the aedeagal apex and is used as a noun in apposition.

**Types.**—Holotype ♂ from Costa Rica, Alajuela, Rio Bochinche, Cerro Campana, 600 m, 22 Jul 1987, R. Holzenthal, J. Morse, P. Clausen (USNM). Paratypes:

Costa Rica: Alajuela: Reserva Forestal San Ramon, Rio San Lorencito, 1090 m, 2–4 Jul 1986, R. Holzenthal, M. Heyn, B. Armitage, 1 ♂ (UMSP). Same location, 24–27 Feb 1987, I. Chacon, A. Chacon, 1 ♂ (USNM). Guanacaste: Estacion Maritza, Rio Tempisquito, 14 Jan 1990, 2 ♂



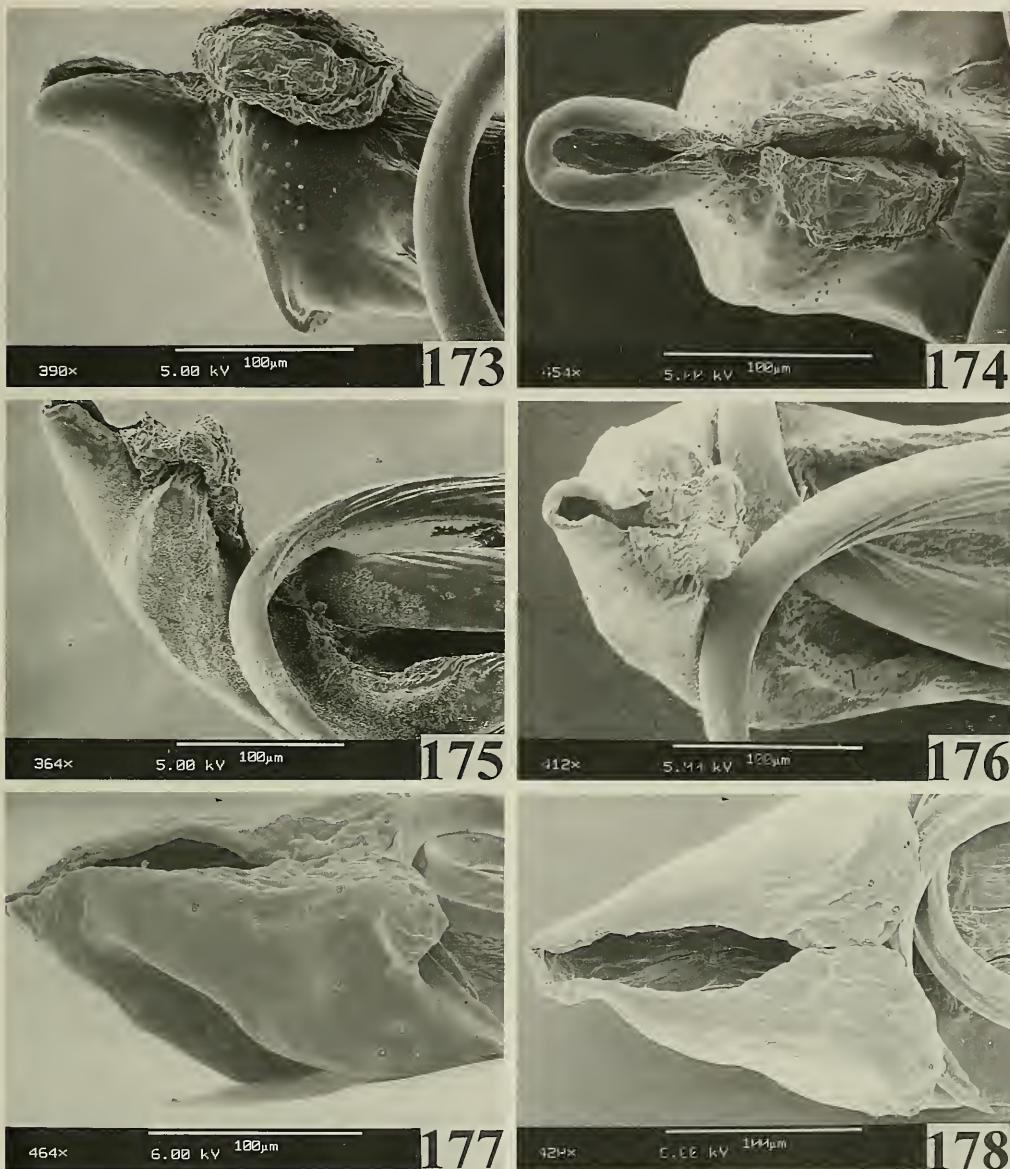
Figs. 167-172. *Anacroneuria* aedeagal structures. 167. *A. divisa* apex, lateral. 168. *A. divisa*, apex, ventral. 169. *A. hacha* apex, lateral. 170. *A. hacha* apex, ventral. 171. *A. holzenthalii* apex, lateral. 172. *A. holzenthalii* apex, ventral.

(SWRC). Same location, 17 Mar 1989, 1 ♂ (SWRC). Same location, 24 May 1989, 1 ♂ (INBIO). Same location, 22 Oct 1990, 3 ♂ (BPS, SWRC). Puntarenas: Rio Bellavista, ca. 1.5 km NW Las Alturas, 1400 m, 8 Apr 1987, R. Holzenthal, S. Hamilton, M. Heyn, 2 ♂ (USNM, UMSP).

*Diagnosis*.—See under *A. marca*.

*Anacroneuria zarpa*, new species  
Figs. 131-135

*Adult habitus*.—Head patterned with diffuse brown over most of frons; lappets



Figs. 173–178. *Anacroneuria* aedeagal structures. 173. *A. magnirufa* apex, lateral. 174. *A. magnirufa* apex, ventral. 175. *A. marca* apex, lateral. 176. *A. marca* apex, ventral. 177. *A. marginata* apex, lateral. 178. *A. marginata* apex, ventral.

brown. Median pronotal stripe yellow, irregular lateral stripes pale brown with scattered rugosities; marginal rim black (Fig. 131). Wing membrane transparent, veins brown.

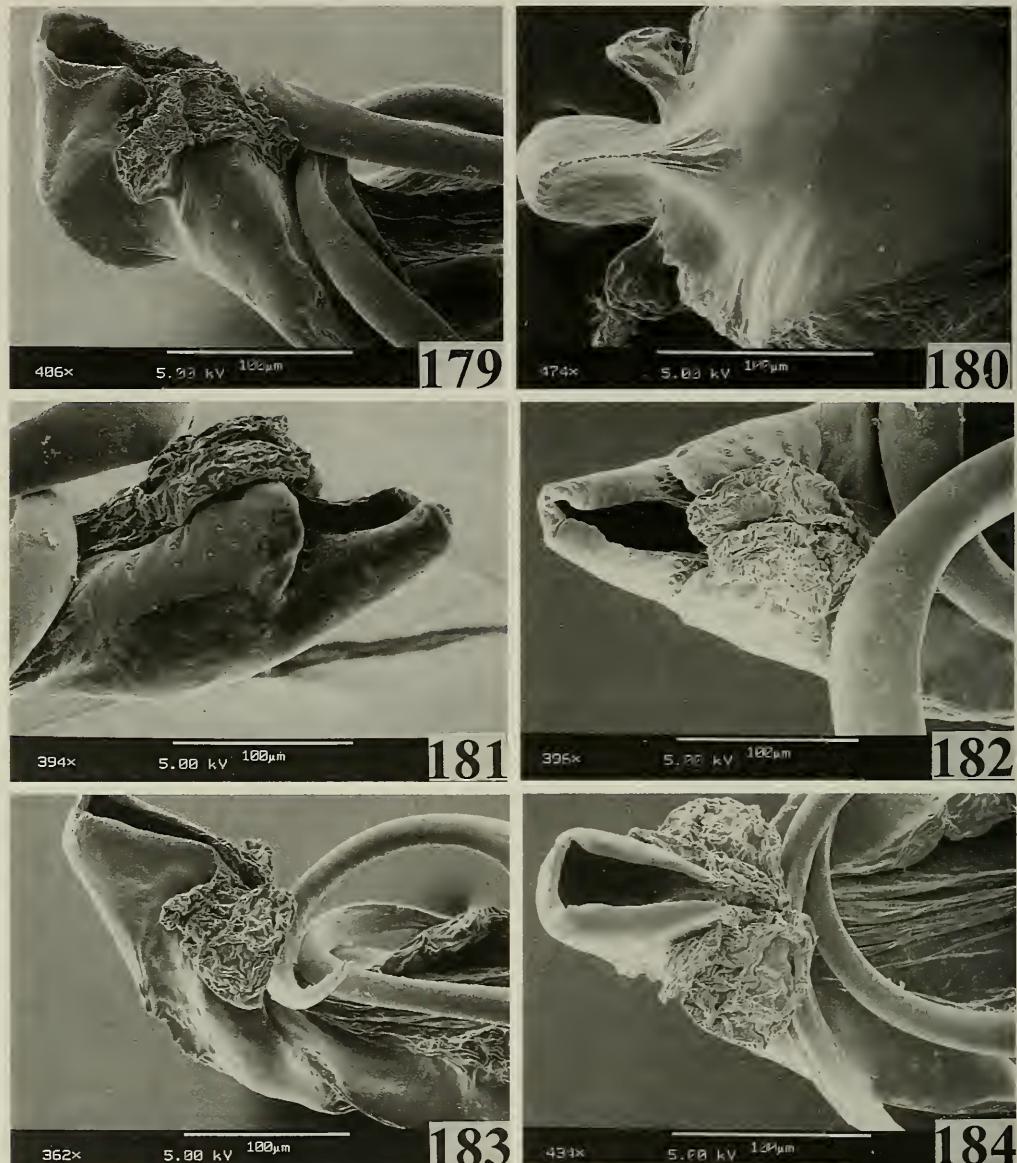
**Male.**—Forewing length 10 mm. Hammer thimble shaped, height subequal to basal diameter (Fig. 132). Aedeagal apex

weakly trilobed and bearing a pair of dorsolateral clawlike lobes. Ventral aspect bearing prominent membranous lobes; tip rounded, hooks slender, keel absent (Figs. 133–135).

**Female.**—Unknown.

**Nymph.**—Unknown.

**Etymology.**—Zarpa, Spanish for claw, re-



Figs. 179-184. *Anacroneuria* aedeagal structures. 179. *A. perplexa* apex, lateral. 180. *A. perplexa* apex, dorsal. 181. *A. plutonis* apex, lateral. 182. *A. plutonis* apex, ventral. 183. *A. varilla* apex, lateral. 184. *A. varilla* apex, ventral.

fers to the clawlike dorsolateral lobes of the aedeagal apex and is used as a noun in apposition.

**Types.**—Holotype ♂ from Panama, Bo-  
cas del Toro Province, Miramar, 21 Feb  
1978, H. Wolda (USNM).

**Diagnosis.**—The color pattern of this species is not particularly distinctive but the

bladelike dorsolateral aedeagal lobes (Fig. 134) distinguish this species from others.

#### Nomina dubia

##### *Anacroneuria antica* (Navas, 1924:71).

Type locality Costa Rica.

The holotype ♀ is severely damaged. Be-

nedetto (pers. comm.) provided notes of an attempted artistic "reconstruction" of the subgenital plate. Despite this I am unable to recognize this species.

*Anacroneuria fulvipennis* (Navas, 1934:17).

Type locality San Jose, Costa Rica.

The holotype ♀ is in fragments and details of the subgenital plate are obscured (Benedetto, pers. comm.).

*Anacroneuria proxima* Klapálek, 1923:23.

Type locality Surrubres, Costa Rica.

The syntypes consisting of a male and female from Costa Rica and a Mexican female have not been located (Benedetto, pers. comm.).

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